SCLEROCACTUS (CACTACEAE): A REVISION

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Summary. The genus *Sclerocactus* Britt. & Rose (Cactaceae) is a small group of globose to subcylindric cacti, mostly with hooked central spines, of the Colorado Plateau, Great Basin, and northern Mojave Desert of the western U.S. Thirteen species and five subspecies are recognized. A new name, *S. cloveriae*, is proposed for the combination of two former varieties of *S. whipplei*, var. *heilii* and var. *reesii*. We also elevate *S. pubispinus* var. *sileri* and *S. wetlandicus* var. *ilseae* to specific status, and describe one new subspecies (*S. cloveriae* subsp. *brackii*). Half of the recognized taxa of *Sclerocactus* are either protected as endangered or threatened species or (in the case of all of the newly described taxa) warrant protection, and we briefly discuss the conservation of this group.

Introduction

Britton and Rose (1922) were the first to recognize the genus *Sclerocactus*, characterizing it by the nearly naked fruit and tuberculate seeds. They included only two species: *S. whipplei* (Engelm. & Bigelow) Britt. & Rose and *S. polyancistrus* (Engelm. & Bigelow) Britt. & Rose. Although new species of *Sclerocactus* were described in the intervening years (Evans, 1939; Clover and Jotter, 1941; Clover, 1942; Peebles, 1949), the first comprehensive study of *Sclerocactus* was that of Benson (1966a, 1966b). In his revision he discusses six species and three varieties (five new combinations and one new species) and provides descriptions, a taxonomic key, and distribution charts. Further work (Woodrull and Benson, 1976; Benson, 1982) expanded the genus to include eight species and two varieties. No fewer than five species and three varieties have been described (Castetter et al., 1976; Heil, 1979; Welsh and Thorn, 1988; Heil and Welsh, 1988; Hochstätter, 1989, 1993) that were either not evaluated by Benson or post-date his work. Although there has been one attempt to re-evaluate this genus since Benson (1982), Hochstätter (1993) falls short of a systematic revision, for the herbaria of the United States were not consulted nor the type collections reviewed.

The circumscription of this genus as a whole is not without controversy. Gerald Arp (1972) transferred some members of *Sclerocactus* (he did not transfer *S. pubispinus* (Engelm.) L. Benson or *S. parviflorus* Clover & Jotter) into *Pediocactus*, based on the results of a phenetic analysis using an unspecified similarity measure. He concluded that his phenetic analysis provided evidence that both *Sclerocactus* and *Pediocactus* were polyphyletic and should therefore be treated as a single genus. Unfortunately, Arp confused overall similarity with synapomorphy (similarity due to the possession of shared derived features) as providing evidence of phylogenetic relationships (Hennig, 1966). Moreover, he failed to include other taxa which may be more closely related to *Sclerocactus* than to *Pediocactus* (e.g., *Echinomastus*). Without taxa to serve as outgroups, there is no way to demonstrate monophyly of his circumscription of *Pediocactus* or to root his tree, rendering his conclusions hollow. The different method of fruit dehiscence, dissimilarities in seed structure, anther ultra-structure and persistent versus nonpersistent perianths easily distinguish *Sclerocactus* from *Pediocactus* (Benson, 1974; Heil et al., 1981; Heil and Porter, unpubl.). In a more recent recircumscription of the genus, the International Organization of Succulent Plant Study (IOS) has taken a more conservative view, including *Ancistrocactus, Echinomastus, Toumeya, Glandulicactus,* and *Homalocephala* in *Sclerocactus*, based on similarities in seed morphology (Hunt and Taylor, 1986); *Pediocactus*, however, was not included in *Sclerocactus*.

We have taken a more traditional view of *Sclerocactus* by regarding *Pediocactus, Ancistrocactus, Echinomastus, Toumeya, Glandulicactus* and *Homalocephala* as distinct genera, even though there is evidence that some of these groups (or members thereof) may be closely related to *Sclerocactus*. Further research into the anatomy, morphology, development and phylogeny of these groups will clarify their relationships. However, in the meantime, because these data are largely lacking, it seems premature to include other recognized genera in *Sclerocactus*.

High levels of morphological variation within and between populations of the recognized species, and shifts in morphology during life (juvenile vs. reproductive, primary stem vs. secondary stems) have made *Sclerocactus* a notoriously difficult group for species-level identification. This variation may involve all parts of the plant body including floral, stem and spine features. A noteworthy example is the profound differences between juvenile and mature stems in *Sclerocactus*. The morphology of juvenile (prereproductive) plants is characterized by more

globose or elliptic stems bearing podaria (tubercles) that are not coalesced into ribs. These stems have areoles that either lack central spines or that have short central spines and few, short radial spines. In some species this morphology is maintained throughout the life of the plant (e.g., *S. mesaeverdae* and *S. brevispinus*), but generally all of these features change as the plant matures. Adult (reproductive) individuals have cylindroid stems in which the tubercles are coalesced into distinct ribs, while the areoles bear a greater number of longer central and radial spines. There appears to be a repeated pattern of morphological change in *Sclerocactus*. This involves the tendency in some populations (or species) for reproductive individuals to bear stem and spine features found in juveniles of other populations or species. Remarkably, these populations also possess convergent floral morphologies: flowers are short, broad and barrel-shaped, with ovoid tepals, and somewhat resemble an open bud. This convergent floral morphology should not be surprising; any change in stem development will also affect the flowers, for part of the flower (i.e., the pericarpellary region) is derived from stem tissue. The change in timing of events during development (heterochrony) in which plants that appear juvenile vegetatively are able to flower and fruit, is termed paedomorphosis. It appears that paedomorphosis plays an important role in the evolution of *Sclerocactus*.

This revision is the first comprehensive study of *Sclerocactus* since Benson (1966a, 1966b, 1982) and is an attempt to make some sense of the patterns of morphological variation in light of more extensive population-level field-work (the senior author began his study of *Sclerocactus* more than twenty years ago). This field-work has provided a better understanding of the distribution of the species and the patterns of morphological variation with respect to geography. We hope to provide a more uniform treatment of the inter- and intra-population patterns of morphological variation and to designate those morphologically cohesive units that possess geographic and ecological continuity. This treatment provides a springboard from which future studies can be launched, testing both the classification presented here and the relationships between these and other cacti. Although there has been great interest in this group, owing largely to the rarity of some of its members, very little biological data exists in the literature. It is our hope that this treatment will stimulate further research of reproductive biology, genetic structure of populations, physiology, and structural anatomy within *Sclerocactus*.

Although about half the species of *Sclerocactus* are widespread and quite plentiful, six have restricted ranges. Three are listed by the United States Fish and Wildlife Service (USF&WS) as threatened or endangered: *S. mesae-verdae*, *S. glaucus*, and *S. wrightiae*. In addition, two species, (*S. brevispinus*, and *S. sileri*) and one subspecies (*S. cloveriae* subsp. *brackii*) are very limited in distribution and should be considered rare and potentially in need of federal protection. With current world attention focused more and more on conservation issues, it is ironic that it is necessary to stress the need for restraint from field collection of these rare species. Illegal taking of federally protected cacti has continued over the years, including the removal of plants from scientific study-plots designed to evaluate the demography and biology of these endangered plants. Because of concerns over protection, we have found it necessary to limit the citation of specimens, particularly for uncommon species, and to be vague at times in discussions relating to distribution. We would like to point out that the collection of federally listed species is a violation of federal law; the collection of any sclerocactus on tribal lands is a violation of Navajo Tribal law; and collection of this genus on Ute Mountain, Ute Indian lands, Southern Ute Indian lands, or Uintah and Ouray Indian lands, is a violation of tribal law.

Sclerocactus

Sclerocactus Britt. & Rose, Cactaceae 3:212. 1922. Type species: *Sclerocactus polyancistrus* (Engelm. & Bigelow) Britt. & Rose (Benson [1966] designates *S. whipplei* as type; however, Britton and Rose [1922:212] clearly designate a type: "... *Echinocactus polyancistrus* is the type"). *Coloradoa* Boissevain in Boissevain & Davidson, Colorado Cacti 54. 1940. Type species: *C. mesae-verdae* Boissevain ex Hill & Salisbury. *Ferocactus* section Sclerocactus (Britt. & Rose) N. P. Taylor, Cact. Succ. J. (Gr. Br.) 41:90. 1979.

Perennial, stems succulent, plant deep-seated in winter but never flat-topped. *Stems* mostly solitary, occasionally clumped, pale green to dark green, or bluish green, occasionally glaucous, ovoid, globose, or depressed-globose, depressed-hemispheric, cylindroidal to elongate-cylindroidal, 1.8–15 cm diam, 1–40 cm long; *podaria* usually coalescent (forming 10–17 ribs), rarely remaining separate (tubercles), mostly 6–14 mm long vertically, 6–9 mm broad; *areoles* elliptic; central and lateral *spines* (0) 1–6(–11), gray, white, yellow, straw, red, reddish-brown, brown, pink to purplish-pink or black, usually of two or three distinct types and usually one or more hooked, the longer 0.7–9 cm long, 0.5–3 mm thick, acicular or subulate or commonly some of each type; radial spines 2–11(–18), white or gray or sometimes straw, brown pink or purplish-pink, 0.6–6 cm long, straight; *flowers* near apex of stem, opening 1–6 cm wide, 1–5.7 cm long; floral (receptacular) tube funnelform; *bracteoles* soft and scale-like, succulent, margins hyaline, entire or fimbriate, axils naked or sparsely hairy; *outer tepals* with greenish-lavender, reddish-brown,

yellowish-brown, or purple midstripes, the margins white, cream, gold, rose, pink, or purple, oblanceolate, 1–4.5 cm long, 3–10 mm wide; *inner tepals* white, yellow, or pink to reddish-purple, red violet, magenta or lavender, lanceolate to oblanceolate, 1.5–5 cm long, 4–12 mm wide; *filaments* white, cream, green, pale yellow, purple or magenta, the anthers yellow or rarely cream, margin of dehisced thecae with long papillae; *style* cream, light green, pink or purple, papillose throughout in all species except *S. polyancistrus*; stigma green to yellowish-green, 7–12-lobed; *pericarpel* epidermis with large papillae and appearing granular, or with small papillae and appearing smooth; *fruits* from near stem-apex, green, often turning red, thin-walled, becoming dry at maturity, naked or with a few broad, thin scales, 0.7–3 cm long, 0.5–2.1 cm diam, opening with 2–4 irregular, short, vertical slits above the base within a nearly regular, circular region around the base, or indehiscent; *seeds* brown or black, papillate-reticulate, rarely furrowed, 1.5–3 mm long (maximum length), 1.9–4 mm broad, 1–1.5 mm thick.

The thirteen species included in *Sclerocactus* are found in the southwestern United States in the Great Basin and Colorado Plateau provinces. In the Mojave, Great Basin, and Navajoan Deserts they are associated with blackbrush, saltbrush, sagebrush, and pinyon-juniper woodland communities. In the Death Valley region, *S. polyancistrus* grows at an elevation as low as 2500′ (758 m), while in San Juan County, New Mexico, *S. cloveriae* has been found as high as nearly 8000′ (2420 m). These species occur on many different soil-types, ranging from very gravelly, sandy soils to heavy, alkaline clays, or gypsiferous soils.

Key To The Species of *Sclerocactus*

1. Central spine 0–1; perianth cream or pink; clay soils; in southwestern Colorado and northwestern New Mexico. ..... 1. *S. mesae-verdae.*
1. Central spines 1–11 (rarely 0 in Duchesne County, Utah); perianth color various; on various soil types. ..... 2.
   2. Filaments magenta, flowers pale pink to whitish, fruit usually lacking bracts; south-central Utah. ..... 2. *S. wrightiae.*
   2. Filaments green to whitish, but if magenta then tepals purple, not pale pink or whitish; fruit often bearing bracts. ..... 3.
      3. Lower central spine either not hooked, absent, or, if slightly hooked, then less than 1 cm long; restricted to clay soils. ..... 4.
         4. Lower central spine mostly straight (rarely hooked); flowers mostly 4–5 cm diam, 3–4 cm long; extreme eastern Utah, southwestern Colorado. . 3. *S. glaucus.*
         4. Lower central spine absent or if present then slightly hooked and less than 1 cm long; flowers mostly 1.75–3 cm diam, 2.5–3.5 cm long; Duchesne Co., Utah. .... 4. *S. brevispinus.*
      3. Lower central spine hooked, over 1 cm long; on various soil types. ..... 5.
         5. Fruit opening along 2–4 vertical slits; central and lateral spines mostly 4; Great Basin Desert and Arizona Strip. .... 6.
            6. Juvenile spines and areoles white-pubescent at the base of older stems; style pink to reddish-violet; Great Basin Desert. ..... 7.
               7. Flowers bronze to yellow; lower central spine red to almost black, 1.5–3 cm long; upper central spines 0.7–3.5 cm long, 0.7–1 mm wide. ..... 8. *S. pubispinus.*
               7. Flowers pink, rose to violet; lower central spine white, gray tan, or almost brown or reddish brown to black, 2–4.5 cm long; upper central spines 2–6 cm long, 1–2.5 mm wide. ..... 8.
                  8. Lower central spine tan to almost brown or reddish to almost black, 2–3 cm long; upper central spine 2–6 cm long, 1–1.6 mm wide; southwestern Utah. .....9. *S. spinosior.*
                  8. Lower central spine white, tan, gray or black, 2.5–4.5 cm long; upper central spine 3.5–5.5 cm long, 1–2.5 mm wide; Iron County, Utah; Nye and Lincoln counties, Nevada. .... 10. *S. blainei.*
            6. Juvenile spines and areoles not white-pubescent; style yellowish-green; Arizona Strip. ..... 11. *S. sileri.*
         5. Fruit indehiscent or dehiscing along a basal suture; central spines 4–8; Mojave Desert and Colorado Plateau. ..... 9.
            9. Hooked spines 1–3; flowers rose, pink, purple, yellow or white; Colorado Plateau. ..... 10.
               10. Flower 3–5.7 cm long, 2.5–5.5 cm wide, funnelform, pericarpel with large papillae, surface granular; upper central spine flat or angled. ..... 5. *S. parviflorus.*
               10. Flower 2.2–3.2 cm long, 1.5–2 cm wide, turbinate, pericarpel with small papillae, smooth; upper central spine flat and ribbon-like. ..... 11.
                  11. Tepals yellow; central spines 4; northeastern Arizona and San Juan County, Utah. .. .. 6. *S. whipplei.*
                  11. Tepals purple; central spines 6–9; southwestern Colorado and northwestern New Mexico. ..... 7. *S. cloveriae.*
            9. Hooked spines 4–8; flowers rose purple to magenta; Mojave Desert. .12.
               12. Stems mostly 10–20 cm long; central spines 9–11; flowers mostly 5 cm wide, 5–6 cm long; seeds finely papillate. .... 12. *S. polyancistrus.*
               12. Stems mostly 5–10 cm long; central spines 4–7; flowers mostly 2–2.5 cm diam, 3–4 cm long; seeds irregularly furrowed. .... 13. *S. nyensis.*

1. ***Sclerocactus mesae-verdae*** (Boissevain ex Hill & Salisbury) L. Benson, Cact. Succ. J. (U.S.) 38:54. 1966.

Coloradoa mesae-verdae Boissevain ex Hill & Salisbury, Index Kewensis Suppl. 10:57. 1947. (not *Coloradoa mesae-verdae* Boissevain ex Boissevain & Davidson, Colorado Cacti 55. 1940); *Echinocactus mesae-verdae* (Boissevain ex Hill & Salisbury) L. Benson, Leafl. West. Bot. 6:163. 1951. *Sclerocactus mesae-verdae* (Boissevain ex Hill & Salisbury) L. Benson, Cact. & Succ. J. (U.S.) 38:54. 1966. *Pediocactus mesae-verdae* (Boissevain ex Hill & Salisbury) Arp, Cact Succ. J. (U.S.) 44:222. 1972.

Type. *Boissevain s.n.*, Cortez, Colorado (the type specimen was reportedly deposited at the Dudley Herbarium of Stanford University; however, it was not found by Benson in 1965. He therefore designated a neotype: *L. E. & R. Benson 16155*, southwest of Mesa Verde, south of Cortez, Colorado, April 11, 1962 (POM 306837).

Mesa Verde Cactus (Fig. 7)

Taproot much branched; *stems* mostly pale green, depressed-globose to ovoid, mostly 3.2–11 cm long, 3.8–8 cm diam; ribs 13–17; *tubercles* inconspicuous; areoles woolly; central *spines* 0(–1), rarely hooked, 7–15 mm long; peripheral spines none; radial spines 7–13, straw-colored, spreading, 6–13 mm long; *flower* 1–3 cm wide, 1–3.5 cm long, diurnal; *outer tepals* with purple midstripes and cream or gold margins, oblanceolate, 1–2.5 mm long, 5–8 mm wide; *inner tepals* yellow to cream, rarely pink, oblanceolate, 1.5–3 cm long, ca. 5 mm wide; *filaments* pale yellow or white; anthers yellow; *style* light green, densely papillate; stigma green, 7–9 lobed; *fruit* green, becoming tan at maturity, short cylindroid, 8–10 mm long, indehiscent; *seeds* black, 2.5–3 mm long, 3–4 mm wide.

Distribution. Extreme southwestern Colorado and northwestern New Mexico.

Representative Specimens. COLORADO: MONTEZUMA CO. Southwest side of southern attenuation of Mesa Verde; near base of the prominent butte; bare hills, *L. Benson*, April 11, 1962 (POM 306837). NEW MEXICO: SAN JUAN CO. Ca. 6 mi south and 0.5 mi east of Shiprock, New Mexico, *K. Heil*, July 1979 (SJNM 2649).

The Mesa Verde cactus was discovered by Charles Boissevain in Colorado and described and published in 1940. It grows on the tops, sides, and base of Mancos clay hills between Cortez, Colorado and Sheep Springs, New Mexico, at an elevation range of 4900–5500′ (1480–1660 m). Associated plants include *Opuntia polyacantha* (prickly pear cactus), *Atriplex corrugata* (mat saltbush), *Atriplex confertifolia* (shadscale), and *Frankenia jamesii* (frankenia). *S. mesae-verde* usually occurs in full sunlight but may grow under a desert shrub. During periods of winter dormancy, the Mesa Verde cactus retracts into the soil, though on mature plants at least some part of the stem is exposed. During early spring the plant emerges and begins blooming in late April or early May.

Table 1. Species and varieties of *Sclerocactus*

1. *Sclerocactus mesae-verdae*
2. *S. wrightiae*
3. *S. glaucus*
4. *S. brevispinus*
5. *S. parviflorus*
   A. subsp. *parviflorus*
   B. subsp. *intermedius*
   C. subsp. *terrae-canyonae*
6. *S. whipplei*
7. *S. cloveriae*
   A. subsp. *cloveriae*
   B. subsp. *brackii*
8. *S. pubispinus*
9. *S. spinosior*
10. *S. blainei*
11. *S. sileri*
12. *S. polyancistrus*
13. *S. nyensis*

Sclerocactus mesae-verdae is one of the more distinctive and morphologically invariant species of this genus. Even so, there is some population-level variation; notably, populations at the southern extreme of the range tend to possess pink flowers, rather than the more typical yellowish-cream flowers. There is also a well documented, sporadic mutation with a single hooked central spine per areole.

The pollination biology of *S. mesae-verdae* has been examined by Tepedino (unpubl., pers. comm.) at the Bee Biology & Systematics Laboratory, Utah State University. His research indicates that this species is predominately outcrossing, though self-compatible. Pollen from the same flower (autogamy) does not produce seed, but pollen from a different flower on the same plant (geitonogamy) frequently results in seed-set. However, seed production from geitonogamous pollinations produced 50% fewer seed than outcrossed (xenogamous) pollinations. This indicates that some pollination vector is required for successful seed-set in *S. mesae-verdae*. Flowers open from mid-morning to early afternoon and remain open for about seven or eight hours. Each flower opens daily for three to five days, during which the sweetish fragrance disappears. When the flowers first open the anthers are appressed to the style and slowly draw away, already having shed some pollen. Pollen release occurs over several days as the anthers sequentially dehisce from the outer stamen to the inner. Although 22 species of insect visitors (18 native)

were documented by Tepedino (pers. comm.) on *S. mesae-verdae*, the most frequent visitors were small, solitary bees, members of the Halictidae (*Halictus* and *Dialictus*) and Anthophoridae (*Tetralonia*). Included among the insect visitors were two undescribed bees belonging to the genera *Andrena* and *Tetralonia*.

S. mesae-verdae is listed as a threatened species by United States Fish and Wildlife Service (44 FR 62471; October 30, 1979) and is also protected by Navajo Nation laws. In spite of this protection, the illegal taking of this species from the wild continues.

2. ***Sclerocactus wrightiae*** L. Benson, Cact. Succ. J. (U.S.) 38:55. 1966.

Pediocactus wrightiae (L. Benson) Arp, Cact. Succ. J. (U.S.) 44:221. 1972.

Type. *L. & E. Benson 16595*; near San Rafael Ridge, Emery Co., Utah, ca. 5000'; Navajoan Desert (POM 311309).

Wright's Fish-hook Cactus (Figs. 8, 19)

Taproot much branched; *stems* mostly pale green, depressed-globose, 1–8 cm long, 4–8 cm diam; ribs 13–16; tubercles to 12 mm long, 9 mm broad; central *spines* 4, the lower one hooked, mostly white or rarely tan to black 1–3(–4.4) cm long, 0.5–1 mm broad, lateral upper spines 2, mostly white or brown to reddish-brown to black, 1–2.1(–3.5) cm long, 0.8–1.5 mm wide; upper central white, 0.6–2.7(–3.5) cm long, 0.5–1.5 mm wide, flat to angled; radial spines 5–10(–14) white, 0.6–1.7 cm long; *flower* 3–4 cm diam, 3–4 cm long, fragrant; *outer tepals* with reddish-brown midstripes and white to cream or pinkish margins, oblanceolate, 1.3–2.3 mm long, 3–7 mm wide; *inner tepals* white to cream or pink, oblanceolate, 2.5–3 cm long, 5–7 mm wide; *stamens* with magenta filaments; anthers yellow; *style* green, papillose; stigma green or yellowish-green, 7-lobed; *fruit* barrel-shaped, 9–12 mm long and thick; *seeds* black, 2 mm long, 3.5 mm broad.

Distribution. South-central Utah.

Representative Specimens. UTAH: EMERY CO. Goblin Valley, *D. Wright* 1961 (*POM* 306389). 3 mi east of Sevier Co. line, 4.5 mi south of I-70 at 6050', *E. Neese*, 20 May 1982 (NY). Last Chance Wash in the San Rafael Swell, *R. Kass*, 21 May 1989 (BRY 328910). WAYNE CO. Capitol Reef National Park, 0.2 mi NW of Ackland Spring, *R. Fleming*, 03 May 1987 (SJNM 7415).

Wright's fish-hook cactus grows on clay hills near the Fremont River and San Rafael Swell at an elevation range of 4600–6000' (1400–1800 m). The cactus is usually found exposed to full sunlight on highly alkaline and often bare clay hills. Like the Mesa Verde cactus, *S. wrightiae* retracts into the soil during periods of winter dormancy. During the early spring, after sufficient rainfall, the plant fully emerges and blooms in late April or early May. This sclerocactus has unusually fragrant flowers. Associates include *Atriplex* sp., *Eriogonum* sp., *Phacelia demissa* and, rarely, *Pediocactus winkleri* and *Townsendia aprica*. Benson suggests that *S. wrightiae* and *S. mesae-verdae* are closely related and that Wright's fish-hook cactus is a connecting link between *S. mesae-verdae* and *S. parviflorus* (Benson, 1982). *S. wrightiae* is probably more closely related to *S. parviflorus* than to *S. mesae-verdae*, and the similarity between *S. mesae-verdae* and *S. wrightiae* is likely the result of convergence caused by independent but similar changes in evolution. These paedomorphic events, or truncations of ancestral developmental pathways, may represent adaptations to particular edaphic sites, in particular, saline or gypsiferous clay badlands. These habitats harbor several species that appear to be locally restricted, independent paedomorphic derivatives of more widespread taxa and could be regarded as edaphic endemics (Mason, 1946a, 1946b).

Recent studies of the distribution of *Sclerocactus wrightiae* reveal that this species is considerably more variable than was once believed and it has been suggested that it hybridizes with *S. parviflorus* (Neese, unpubl.; Welsh et al., 1987). Some populations, particularly those on heavy clay, have depressed-globose stems with short spines and short, somewhat barrel-shaped, pale pink flowers. At the other extreme, on more sandy soils, individuals are more elliptical to cylindroidal, possessing longer spines, and longer, more funnelform, whitish flowers. In all of the populations, however, the flowers possess stamens with magenta-colored filaments.

Wright's fish-hook cactus is listed as endangered by the United States Fish and Wildlife Service (44 FR 58868; October 11, 1979).

3. ***Sclerocactus glaucus*** (J. A. Purpus ex K. Schum.) L. Benson, Cact. Succ. J. (U.S.) 44: 221. 1972.

Echinocactus glaucus J. A. Purpus, Monatsschr. Kakteenk. 5:106. 1895. *Echinocactus glaucus* J. A. Purpus ex K. Schumann, Gesamtb. Kakteen. 438. 1898, not Karwinsky ex Pfeiffer, Enum. Diag. Cact. 57. 1837. *E. subglaucus* Rydberg, Fl. Rocky Mtns. 580. 1917. *E. whipplei* Engelmann & Bigelow var. *glaucus* (J. A. Purpus) J. A. Purpus, Mitt. Deutsch. Dendr. Gesellsch. 1925:50. 1925. *Sclerocactus whipplei* (Engelm. & Bigelow) Britt. & Rose var. *glaucus* (J. A. Purpus) S. L. Welsh, Great Basin Nat. 44:68. 1984. *Sclerocactus glaucus* (J. A. Purpus) Backeberg, Cactaceae 5:2683. 1961 (according to Benson, 1982, invalidly published). *Sclerocactus glaucus* (J. A. Purpus) L. Benson, Cact. Succ. J. (U.S.) 38:53. 1966. *Pediocactus glaucus* (J. A. Purpus) Arp, Cact. Succ. J. (U.S.) 44:221. 1972.

Type. *Purpus 60a, 61, 64* (syntypes); in Colorado auf der Mesa Grande, am Dry Creek bei 1800 m. *Purpus, 62* (syntype); bei Gummison (sic): derselbe n. 62. These specimens were originally deposited at the Berlin Museum but were destroyed during the Second World War (Benson, 1982). Lectotype: C. A. Purpus, Juni 1892. Arboles am Dry Creek Mesa Grande, Delta Co. Höhe über dem Meer: 5–6000' (F 357488).

Sclerocactus franklinii J. W. Evans, Cact. Succ. J. (U.S.) 11:74. 1939.

Type. South rim of Gunnison Valley, one or two miles east of Delta, Delta County, Colorado; 5000' (DS 255234).

Sclerocactus wetlandicus Hochst. Succulenta 68:124. 1989. (Excl. var. *ilseae*).

Uinta Basin Hookless Cactus (Fig. 9)

Taproot much-branched; *stems* mostly solitary, bluish-green (glaucous), cylindroidal to elongate-cylindroidal, 3–12 cm long, 4–9 cm wide; *ribs* 12–13; *tubercles* up to 9 mm long, 6–9 mm broad; spines not obscuring the stem, the centrals 1–5, the upper central mostly white, rarely light brown, 1.5–3.1 cm long, 0.5–1.75 mm wide, elliptic in cross section, lower central spine up to 2, brown, reddish-brown to black, 1.2–2.6 cm long, 0.8–1 mm wide, mostly straight but may be curved or hooked; radial spines white, 2–6, 0.6–1.7 cm long; *flower* 4–5 cm diam, 3–4 cm long, fragrant; *outer tepals* with greenish-lavender midribs and pink margins, oblanceolate, 2.5 cm long, up to 6 mm broad; *inner tepals pink*, lanceolate, up to 3 cm long and 6 mm broad; *stamens* with green filaments; anthers yellow; *style* up to 2 cm long, papillose, stigma 0–12-lobed; *fruit* barrel-shaped, 9–12 mm long, ca. 9 mm diam; *seeds* black, 1.5 mm long, 2.5 mm broad.

Distribution. Northeast Utah near the Green River; Colorado from near Grand Junction south to near Montrose.

Representative Specimens. COLORADO: DELTA CO. Below Dominguez Rim, *K. Heil*, 1986 (SJNM 6909). East rim of Gunnison Valley, *L. & L. Benson*, 1950 (POM 278846). Kanah Creek, *K. Heil & J. M. Porter*, 24 April 1986 (BRY 148169). GARFIELD CO. Debeque, north of the cemetery, *G. K. Arp*, 20 June 1970 (COLO 248046). MESA CO. Land's End Road, *E. Neese*, 27 May 1983 (BRY 260270). Near Whitewater, along the rim of the Gunnison River, *K. Heil & J. M. Porter*, 24 April 1986 (SJNM 6939). MONTROSE CO. Escalante Canyon at 5200 feet, *G. K. Arp*, 4 September 1971 (COLO 256871). UTAH: DUCHESNE CO. Wrinkles Road, ca. 6 mi W of the Green River, *E. Neese & S. White*, 15 May 1980 (BRY 211871). UNITAH CO. Benches of the Duchesne River, *K. Heil*, 26 April 1986 (SJNM 6955).

S. glaucus is often found growing on clay hills covered with a thin veneer of gravel at an elevation of 4500–6500' (1360–200 m), growing with salt bushes, shadscale, rabbitbrush, galleta grass, Indian ricegrass and sagebrush, and usually in the open.

The Unita Basin hookless cactus was discovered by J. A. Purpus in 1895, and its taxonomic status has been in a state of confusion to the present time. Although it is not recognized at any taxonomic level in the Utah Flora (Welsh et al., 1994), other students of Cactaceae feel that it is either a subspecies of *S. parviflorus* or sufficiently different to warrant recognition as a species. The authors have examined patterns of variation in quantitative morphology (Heil and Porter, 1987; Porter and Heil, in prep.) of this and other members of *Sclerocactus*. We have found statistically significant differences between *S. glaucus* and *S. parviflorus* in most of the morphological characters examined. Morover, the differences are of the same magnitude as the differences between *S. parviflorus* and other species (i.e., *S. wrightiae*, *S. whipplei* and *S. spinosior*). Interestingly, in the few places where *S. parviflorus* and *S. glaucus* are sympatric, *S. glaucus* flowers about two weeks prior to anthesis in *S. parviflorus*.

Sclerocactus glaucus is made up of a surprisingly polymorphic group of populations. This should not be surprising given that there are two centers of distribution, one in northeastern Utah and the other in Colorado, near the Colorado River. As far as is known, there is no connection between these distributional regions and, because pollination vectors are very unlikely to traverse long distances, they are probably genetically isolated as well. Hochstätter erected the name *S. wetlandicus* for the Utah populations of *S. glaucus*. However, nearly all populations differ in mean spine number and length, length of floral parts, and the size and shape of stems, as well as degree of hooking in the lower central spine. Indeed there is greater variation between populations within Utah or Colorado than between the two regions. For example, a few populations occurring on gravels which overlay shale in the canyon bottoms of Dominguez Creek, Colorado, possess very short spines, small flowers and small, depressed globose stems. These plants might be easily mistaken for *S. mesae-verde*, were it not for the short, straight central spines. Not far away, near Kahana Creek, at a site well above the flood plains of the creek, *S. glaucus* appears as tall, cylindroidal plants with dense, long spines and large flowers. These populations, at least in terms of overall size, are reminiscent of *S. parviflorus*. Interestingly, within the respective populations, the morphology is extremely constant: there is little variation within populations but often great variation between populations. A similar pattern of interpopulational variation is found in Utah.

Pollination biology of *S. glaucus* has been investigated by Tepedino (unpubl., pers. comm.), Bee Biology & Systematics Laboratory, Utah State University. This work indicates that this species is predominately outcrossing; however, it is marginally self-compatible, and seed-set from

self-pollination (autogamy) does occur. Flowers open from mid-morning to early afternoon and remain open for about seven hours. Each flower opens daily, for three to five days, during which both the color of the tepals fades and the sweetish fragrance dissipates. When the flowers first open, the anthers are appressed to the style and slowly draw away and begin shedding pollen. Pollen release occurs over several days as the anthers sequentially dehisce from the outer stamen to the inner. Although 17 species of insect visitors were documented by Tepedino (pers. comm.), the most frequent visitors were small solitary bees, members of the Halictidae (*Halictus* and *Dialictus*) and Anthophoridae (*Anthophora* and *Tetralonia*). It should be noted that the exact location of the population under study was not revealed to us; however, it was identified as being south of Myton, Utah, suggesting that this data on reproductive biology may refer to a population of *S. brevispinus*.

S. glaucus is listed as threatened by the United States Fish and Wildlife Service (44 FR 58870; October 11, 1979).

4. ***Sclerocactus brevispinus*** K. D. Heil & J. M. Porter, nom. et stat. nov.

S. wetlandicus Hochstätter var. *ilseae* Hochstätter, Succulenta 72(2):22. 1993.
Type. *F. Hochstätter. JH0700* (HBG).

Figs. 1, 10.

Stems mostly solitary, green, elongate and cylindrical, ovoid when young, 2.9–7.5(–8.5) cm long (mean = 5.5 cm; SD = 1.39), 1.8–6.5(–7.0) cm in diam (mean = 5.2 cm; SD = 0.96); *ribs* usually 13, more or less obscure to well-developed, the upper portion of the *tubercles* evident above the ribs, 5–14 mm long, 4.5–15 mm broad and protruding above the ribs 5–15 mm; areoles 4.5–8.5 mm diam, typically 9–24 mm apart; central *spines* 4(–5), the hooked lower one often absent, but, if present, straw-colored to brown, highlighted purplish or reddish, terete or somewhat angled, hooked, porrect, 0.3–3.1 cm long, ca. 0.5–1.0 mm in diam, turned or curving somewhat downward, the lateral centrals similar to the lower but a bit shorter and not curved, angled to flat, somewhat inconspicuous, triangular in cross section, 1.5–3.5 cm long, 1.0–1.5 mm broad, erect; radial spines 6–7 (5–8), basally 0.9–1.5 mm broad, acicular, elliptic or rhombic in cross-section; *flower* 2.3–3.5(–4) cm long (mean = 3.0; SD = 0.37), 1.6–3.0(–3.5) cm in diam (mean = 2.5 cm; SD = 0.47), exterior floral tube glabrous, not minutely granular-papillate; *outer tepals* greenish to purple with brownish midribs, pink, purple or whitish at the margins, the larger oblanceolate, 10–15 mm long, 3.5–7 mm broad, mucronate, marginally membranous and crisped or minutely toothed; *inner tepals* purple, sometimes suffused with brown, the largest lanceolate, 15–22(–30) mm long (mean = 19.0; SD = 0.20), 4–6 mm at the broadest point (mean = 4.75; SD = 0.09), mucronate, somewhat irregularly toothed; *filaments* white, tinged with pink to pink-purple, 6–10 mm long, anthers yellow, 0.9–1.2 mm long, 0.3–0.5 mm wide; *style* tinged with pink or purple, rarely green, 14.6–19.5 mm long, 1–1.5 mm in diameter, covered with minute but conspicuous papillae; stigma lobes 5–8, ca. 1.2–2.5 mm long, 0.5–1 mm broad; nectary chamber 1.5–2(–3) mm deep; ovary 3–7 mm long at anthesis; *fruit* green to tan, sometimes suffused with pink, dry, with a few membranous, scarious-margined, minutely toothed or fimbriate scales, 7–15 mm long, 5–12 mm broad, irregularly opening just below the middle or along a regular line of dehiscence at the base of the ovary; *seeds* 1.2–2 mm long, 1.9–3 mm broad; hilum not deeply indented.

Distribution. A narrow endemic occurring in a series of small scattered populations in badlands near Myton, Utah.

Representative Specimens. UTAH: DUCHESNE Co. Clay badlands of the Duchesne River Shale, near Parriette Canyon, Duchesne Co., Utah, 5140', *K. Heil & J. M. Porter* SJNM (6911).

It is unclear who first discovered this species; however, two of the first botanists to document populations of *S. brevispinus* were Larry England (United States Fish and Wildlife Service Species Enhancement) and Stan Welsh (Brigham Young University) in the early 1980's. This cactus has long been a curiosity to cactus horticulturists and collectors. It is extremely rare, growing at the base of Duchesne clay hills between 5000–6000 feet elevation. Originally described as a variant of *S. wetlandicus* (Hochstätter's designation of the Utah populations of *S. glaucus* at the specific level), this series of populations represents the only morphologically distinctive element associated with the previously circumscribed *S. glaucus* complex, in spite of apparent introgression.

Morphological intergradation between this species and, presumably, *S. glaucus* has been the subject of several studies by U.S. Fish and Wildlife Service, USDI Bureau of Land Management, and the authors. The distribution of *S. brevispinus* forms a string of populations running east to west. At the western extreme, populations are characterized by plants with depressed-globose stems, short radial spines lacking a lower central (hooked) spine and possessing very short, barrel-shaped, pale-pink-colored flowers. Populations located at about the middle of this string are characterized by plants with globose to more elliptical stems, somewhat longer radial spines, a very short (usually less than 5 mm) hooked lower central spine and flowers that are slightly longer and pink to purple in color. At the eastern extent, some populations appear to be highly introgressed forms and technically should not be considered as *S. brevispinus*. These plants are characterized by elliptical stems and radial and central spines of the same length as in *S. glaucus*; however, the lower central is often hooked, and the flowers are of the same shape and color as in *S. glaucus*. Other populations at the eastern limit of this species display little evidence of introgression.

S. brevispinus is currently under review by the United States Fish and Wildlife Service for listing as a threatened or endangered species (L. England, pers. comm.). There is no question that this species is one of the most restricted taxa of *Sclerocactus*, and there are numerous threats to its continued existence in the wild.

Fig. 1. An extremely rare caespitose form of *Sclerocactus brevispinus*. Duchesne Co., Utah.

5. ***Sclerocactus parviflorus*** Clover & Jotter, Bull. Torrey Bot. Club 68:419. 1941.

Echinocactus parviflorus (Clover & Jotter) L. Benson, Cacti of Arizona, ed. 2:102. 1950.
Type. *Clover & Jotter 2398*, mouth of Forbidding Canyon in Glen Canyon, above Lee's Ferry, canyon of the Colorado. Abundant 20 mi above Moki Creek and fairly common at intervals along the lower San Juan River (MICH, holotype; US 2346042, isotype). = subsp. *parviflorus*.

S. havasupaiensis Clover, Amer. Journ. Bot. 29:172. 1942. *Echinocactus parviflorus* (Clover & Jotter) L. Benson var. *havasupaiensis* (Clover) L. Benson, Cacti of Arizona, ed. 2:104. 1950.
Type. *Clover 6406*. . . . on the top of Supai Formation in Havasupai Canyon, Arizona (MICH, holotype. Isotypes: MICH; US 2346047, 2346049; POM 275262, 311353). = subsp. *parviflorus*.

S. havasupaiensis Clover var. *roseus* Clover, Amer. Journ. Bot. 29:172. 1942. *Echinocactus parviflorus* (Clover & Jotter) L. Benson var. *roseus* (Clover) L. Benson, Cacti of Arizona, ed. 2:102. 1950. *S. whipplei* (Engelm. & Bigelow) Britt. & Rose var. *roseus* (Clover) L. Benson, Cact. Succ. J. (U.S.) 38:104. 1966.
Type. *Clover 6403*. . . . in Havasupai Canyon, Arizona (MICH, holotype. Isotypes: US 2346044, 2346045; POM 275269). = subsp. *parviflorus*.

S. contortus Heil, Cact. Succ. J. (U.S.) 51:25. 1979.
Type. *K. Heil s.n.*, Canyonlands National Park, Utah (UNM 64284, isotype: SJNM). = subsp. *parviflorus*.

Sclerocactus parviflorus Clover & Jotter subsp. ***intermedius*** (Peebles) Heil & Porter, comb. nov.

S. parviflorus Clover & Jotter var. *intermedius* (Peebles) D. Woodruff & L. Benson, Cact. Succ. J. (U.S.) 48:133. 1976.

S. intermedius Peebles, Leafl. West. Bot. 5:191. 1949. *S. whipplei* (Englem. & Bigelow) Britt. & Rose var. *intermedius* (Peebles) L. Benson, Cact. Succ. J. (U.S.) 38:102. 1966.
Type. *Peebles & Parker 14712*, 9 mi SW of Pipe Springs, Mohave Co., Arizona, 5000 ft (CAS 351112. Isotype: ARIZ).

S. parviflorus Clover & Jotter var. *blessingae* W. H. Earle, Saguaroland Bull. 34(3):29. 1980.
Type. *Earle 108791*, Cane Beds, Mojave County, Arizona (ASU. Isotype: DES 18160). = subsp.

Sclerocactus parviflorus subsp. ***terrae-canyonae*** (K. D. Heil) K. D. Heil & J. M. Porter, comb. nov.

S. terrae-canyonae Heil, Cact. Succ. J. (U.S.) 51:26. 1979.
Type. *K. Heil s.n.*, Trachyte Wash, ca. 10 mi S of Natural Bridges Nat'l Monument, San Juan

Co., Utah (UNM 64283. Isotype: UNM 64279, SJNM).

Eagle-claw Cactus

Tap-root solitary branching several times within 2.5–5 cm of the base of the stem; *stems* solitary or clustered, depressed-globose, globose, cylindroid to elongate-cylindroidal, 5–27 cm long, 4.5–13 cm diam; *ribs* (10–)13(–16); *tubercles* 1.5–2 cm apart; *spines* dense, obscuring the stem, central spines 4(–6), the lower central spine hooked, white, straw, light to dark brown, reddish-brown, or pink to purplish-pink or black, 1.5–7.2 cm long, 0.6–1 mm wide, the 2–4 laterals similar to the lower, usually shorter, usually not hooked, the upper central mostly white, rarely gray, straw, pink, or reddish-brown, flat, rhombic or rounded, rarely contorted, 1.7–6.2 cm long, 0.75–1.5(–3) mm wide; radial spines 3–17, mostly white, but may be brown or purplish-pink, 0.6–3.6 cm long; buds pointed; *flowers* mostly apical on upper end of the tubercles near the top of the areole, rarely far below the apex of the stem, 3–5.7 cm long, 2.5–5.5 cm in diameter, pericarpel granular-papillose; *outer tepals* with greenish or brownish purple midribs and rose to purple, pink, yellow, or white margins, oblanceolate, 2.5–4.5 cm long, 6–10 mm broad, mucronate, margins entire; *inner tepals* rose to purple, pink, yellow or rarely white, oblanceolate, 1.5–5 cm long, 6–12 mm broad, mucronate; *filaments* purple, yellow or green, anthers yellow; *style* green or pink to purple, papillose; stigmas 5–10; *fruit* green turning reddish-pink, with a few membranous-fringed scales, 1–2.5 cm long, mostly 1–1.5 cm diam; *seeds* 2.5–3.5 mm diam, 1.5–3 mm long, 1 mm thick, dark brown to black, covered by evenly spaced papillae.

Our treatment of *S. parviflorus* below the species level is only provisional. This species displays a range of morphologies that defies classical approaches to classification. Presumably, the great diversity of form is the result of a combination of limited gene flow between populations and local inbreeding. The treatment here provides a simple method to categorize members of *S. parviflorus*. Unfortunately, we fail to account for the considerable variation within the named subspecies.

Key to the Subspecies of *S. parviflorus*

1. Flowers yellow; upper central spines 1.5 mm wide; pinyon-juniper and sagebrush. ..... subsp. *terrae-canyonae*.
1. Flowers purple to pink-purple. ..... 2.
   2. Upper central spine mostly 1 mm wide; lower Navajoan Desert. ..... subsp. *parviflorus*.
   2. Upper central spine mostly 1.5–2 mm wide; upper Navajoan Desert and pinyon-juniper woodland. ..... subsp. *intermedius*.

5a. ***Sclerocactus parviflorus*** Clover & Jotter subsp. ***parviflorus***.

Fig. 11.

Lower central spine hooked, mostly white or straw, 2–6.3 cm long, 0.6–1 mm diam; upper central spine mostly white or straw, rarely pink, mostly angled, rarely flat or rhombic, 1.7–6.2 cm long, mostly 1 mm wide; petaloid perianth-segments rose or purple. Mostly at lower elevations, 3500–5000′ (1050–1500 m) along major river drainages in the lower Navajoan Desert.

Distribution. Southeastern Utah, adjacent western Colorado, and northern Arizona, mostly along major rivers, i.e., the Colorado, Green, and San Juan.

Representative Specimens. ARIZONA: Coconino Co. Vicinity of Marble Canyon, desert scrub, *R. K. Gierisch*, May 10, 1978 (ASU 100747). Mohave Co. Cedar Ridge, *R. K. Gierisch*, April 23, 1988 (UW 538466). Navajo Co. White Dog Canyon, Skeleton Mesa, *M. A. Wetherrill & W. B. McDougall*, May 9, 1959 (ASC). COLORADO: Mesa Co. Colorado National Monument, 3 mi west of Fruita, *W. Weber*, May 21, 1948 (COLO 3996). UTAH: Emery Co. San Raphael Reef, *J. G. Harris*, April 4, 1980 (BRY 212395). Garfield Co. Near Hole in the Rock, *K. Heil*, April 4, 1977 (SJNM 2694). Grand Co. Northwest end of Castle Valley, *B. Franklin*, May 8, 1985 (BRY 289958). Kane Co. Colorado River at Mile 501/2 above Lee's Ferry, *L. Benson*, June 1, 1963 (POM 315700). San Juan Co. Big Canyon Road in Canyonlands National Park, *K. Heil & J. M. Porter*, April 27, 1986 (BRY 148175). Sevier Co. West of Sevier Co. line, 1 mi S of I-70, *E. Neese & M. Chatterley*, April 4, 1980 (BRY 210963). Wayne Co. Millard Canyon, *S. L. Welsh & J. Holland*, May 10, 1983 (BRY 250570).

S. parviflorus was first collected by Elzada U. Clover and Lois Jotter of the University of Michigan and described in 1941. It is most common along the Colorado River and its tributaries below 4500′ elevation.

S. parviflorus subsp. *parviflorus* is usually found at lower elevations in the Navajoan Desert and is distinguished by its very fine spines. *S. parviflorus* subsp. *intermedius* is most often found in the upper Navajoan Desert and lower pinyon-juniper woodland, usually above 5000′, and has spines that are thicker than in subsp. *parviflorus*. Where these two subspecies meet, intermediate forms are found, presumably the result of interbreeding; however, in regions where the two subspecies are not sympatric, these two subspecies are quite distinct. Subsp. *parviflorus* also hybridizes with subsp. *terrae-canyonae* wherever the two meet.

S. parviflorus subsp. *parviflorus* is often found on sandstone benches and hillsides growing in salt desert shrub and blackbrush communities and in pockets of sand in slickrock communities.

5b. ***Sclerocactus parviflorus*** subsp. ***intermedius*** (Peebles) K. D. Heil & J. M. Porter.

Lower central spine hooked, white, dark brown, reddish-brown, purplish-pink, or black, 1.7–5.9 cm long, 0.5–1 mm diam; upper central spine mostly white, rarely purple to pink, mostly angled, rarely flat or rhombic, 1.9–5.7 cm long, mostly 1.5–2 mm wide; petaloid perianth segments purple, rose, pink or rarely white. Mostly at mid-elevations of 4500–6500′ (1350–1800 m) in the upper Navajoan Desert and pinyon-juniper woodland.

Distribution. Eastern Utah and adjacent Colorado south to northern Arizona, and northwestern New Mexico.

Representative Specimens. ARIZONA: Apache Co. Red Rock Valley, *T. Reeves*, May 30, 1986 (ASU 166501). Coconino Co. Jacobs Pool, below Paria Plateau, *D. G. Davis*, May 19, 1965 (POM 317494). Mohave Co. Vicinity of Cane Beds, *R. K. Gierisch*, April 23, 1988 (NY). Navajo Co. Monument Valley, *R. Craig*, October 1962 (POM 311544). COLORADO: Dolores Co. 7 mi southeast of Dove Creek, *G. K. Arp*, September 6, 1970 (COLO 248353). Mesa Co. 2 mi east of Utah-Colorado state line, *K. Heil*, 24 April 1986 (SJNM 6960). Montezuma Co. McElmo Canyon, *K. Heil*, March 1981 (SJNM 2657). Montrose Co. Just north of Bedrock, Paradox Valley, *W. Weber. G. Kunkel, C. LaFarge*, 2 June 1973 (COLO 269697). San Miguel Co. 4.5 mi northeast of Slick Rock Post Office, *G. K. Arp*, 6 September 1970 (COLO 2-8089). NEW MEXICO: San Juan Co. Shiprock, New Mexico, *K. Heil*, 10 May 1979 (SJNM 2645). UTAH: Carbon Co. Ca. 5 mi east of Wattis, *S. L. Welsh*, 4 June 1981 (BRY 224695). Duchesne Co. West side of Starvation Reservoir near Strawberry Creek, *K. Heil*, 18 May 1983 (SJNM 2207). Emery Co. San Rafael Reef, side canyon of Iron Wash, *J. G. Harris*, 29 May 1980 (NY). Garfield Co. Ca. 3 mi NW of Hite Bridge, *S. L. Welsh*, 28 April 1981 (BRY 224392). Grand Co. 1 mi east of I-70 along the Green River near the town of Green River, *K. Heil*, 23 April 1983 (SJNM 2215). Kane Co. 6 mi SE of Escalante via Hwy 12, *E. Neese*, 31 May 1985 (BRY 292138). San Juan Co. Valley of the Gods, *K. Heil*, 26 December 1978 (SJNM 2669). Sevier Co. Ca. 1 mi north of I-70, T22N, R6E, Sec. 13, *K. Thorne*, 4 April 1980 (BRY 224309). Uintah Co. 4 mi south of Pelican Lake near the Duchesne River, *E. Nesse*, 18 May 1979 (BRY 196888). Wayne Co. Henry Mountains, Sawmill Basin Road south of Hanksville, *E. Neese*, 27 May 1976 (BRY 165690) (Fig. 12).

S. parviflorus subsp. *intermedius* has long been thought of as a variety of *S. whipplei*. L. Benson and D. Woodruff have pointed out the differences (Woodruff and Benson, 1976). Subspecies *intermedius* is most common in the upper Navajoan Desert and pinyon-juniper woodland communities above 4500′ elevation. It frequently hybridizes with subspecies *intermedius* and *terrae-canyonae* where these taxa meet. This subspecies is often found growing in sandy or rocky soils on hillsides, usually in full sunlight. Many plants from Mohave County, Arizona and Kane County, Utah, have the two upper lateral spines hooked.

5c. ***Sclerocactus parviflorus*** subsp. ***terrae-canyonae*** (K. D. Heil) K. D. Heil & J. M. Porter.

Canyonlands Eagle-claw Cactus (Fig. 13)

Lower central spine hooked, mostly white, light brown, reddish-brown, dark brown, or purplish-pink, 2.9–8.2 cm long, 0.75–2 mm diam; upper central spine mostly white or rarely reddish-brown, flat, rhombic or rounded, 2.6–6.2 cm long, mostly 1.5 mm wide; petaloid perianth segments yellow. Mostly at higher elevations, 6500–7500′ (1800–2300 m); upper pinyon-juniper woodland and sagebrush communities.

Distribution. Southeastern Arizona and adjacent Utah.

Representative Specimens. ARIZONA: Coconino Co. Inscription House Trading Post, *J. P. Hester*, June 1950 (POM 306398). Navajo Co. Black Mesa near Moenkope Wash, *J. Klopatek*, 2 June 1982 (ASU 147488). UTAH: Emery Co. Mouth of Temple Mountain, *S. L. Welsh & E. Neese*, 9 May 1984 (BRY 266699). Garfield Co. Henry Mountains, northwest of Bull Mountain along Sawmill Basin Road, *E. Neese*, 30 May 1976 (BRY 165851). Kane Co. North slope above the Paria River, ca. 8 miles south of Glen Canyon City, *N. D. Atwood*, 6 April 1972 (BRY 167176). San Juan Co. Near Muley Point, *K. Heil*, 1 May 1986 (SJNM 6933). Wayne Co. Torrey, Utah, *K. Heil*, September 1979 (SJNM 2622).

S. parviflorus subsp. *terrae-canyonae* was first published at the species level; however, after more investigation and a study of more herbarium material we feel that this taxon is best treated below this level. It is usually found at higher elevations in the upper pinyon-juniper woodland and sagebrush communities, mostly above 6000′ (1800 m) elevation. Subsp. *terrae-canyonae* is often found growing on rocky sandstone soils on hillsides with scattered pinyon and juniper.

6. ***Sclerocactus whipplei*** (Engelm. & Bigelow) Britt. & Rose *Echinocactus whipplei* Engelm. & Bigelow, Proc. Amer. Acad. 3:217. 1857. *Sclerocactus whipplei* (Engel. & Bigelow) Britton & Rose, Cactaceae 3:213. 1922. *Pediocactus whipplei* (Engelm. & Bigelow) Arp, Cact. Succ. J. (U.S.) 44:222. 1972.

   Type. *Bigelow s.n.*, Dec. 3, 1853. Colorado Chiquito (according to Benson, 1982) at Lithodendron Wash, a tributary of the Rio Puerco River, near the Colorado Chiquito, near Petrified Forest National Monument (MO; Isotype POM 317813).

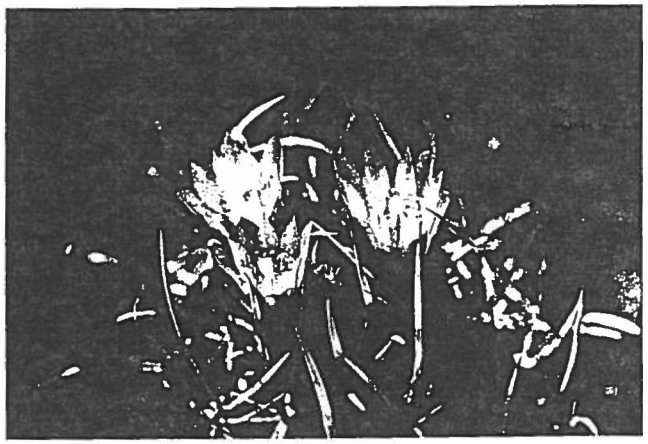


Fig. 2. A close-up of the flat ribbon-like upper central spines and yellow flowers of *S. whipplei*.

S. whipplei (Engel. & Bigelow) Britt. & Rose var. *pygmaeus* Peebles, Leafl. West. Bot. 5:192. 1949.
Type. *Peebles & Smith SF1054*, 15 mi N of Ganado, Apache Co., Arizona, 6200' (CAS 351111).

Figs. 2, 3.

Tap-root solitary branching several times within 2.5–5 cm of the base of the stem; *stems* mostly solitary, depressed-globose, or globose to elongate-cylindroidal, 3–7(–14) cm long, 4–7(–11) cm in diam.; *ribs* formed by confluent tubercles, 13–15; *spines* densely covering the stem; central spines 4, the lower one purplish pink or reddish-brown, somewhat angled, hooked, 1.6–4.5 cm long, 0.5–1 mm in diam, the two lateral spines purplish-pink to white, 1.4–4.5 cm long, mostly 1 mm in diam, the upper one white, mostly flat, dagger-shaped, 1.7–6.5 cm long, mostly 1.5–2(–2.5) mm wide; radial spines 5–12, white except for the two lower, which are mostly purplish-pink, 0.6–2.4 cm long; *flower* buds with blunt tips, shorter than thick, opening in full sunlight; flower 2.2–3.2 cm long, 1.5–2 cm in diam; *outer tepals* with greenish midribs and yellow margins, oblanceolate, ca. 20 mm long, 5 mm broad; *inner tepals* yellow, oblanceolate, ca. 25 mm long, 6 mm broad; *filaments* yellow, anthers yellow, *style* green or green tinged with yellow, papillose, stigma lobes light green, 5–6; *fruit* green or tan, usually reddish at maturity, dry, with a few scarious-margined minutely toothed, membranous-fringed scales, 0.6–1.5 mm in diam, 0.8–2.5 cm long, dehiscing along an irregular cleft, ovoid; *seeds* 2 mm long, 2 mm broad, 1.5 mm wide, pyriform, shiny black.

Fig. 3. *S. whipplei* growing in gravelly soils of the Shinarump Formation, Navajo Co., Arizona.

Distribution. Northwestern Arizona and southeastern Utah.

Representative Specimens. ARIZONA: Apache Co. 2 miles south of Lukachuki on gravely hills, *K. Heil*, 12 May 1986 (SJNM 6938). Coconino Co. 15 mi northeast of Tuba City, *J. & J. Davidson & M. Cazier*. 28 June 1967 (ASU 110953). Navajo Co. Ca. 2 mi northwest of Holbrook, *M. Ganz, D. Pinkava, E. Lehto*. 7 June 1967 (ASU 12391). Agalatha Peak, *K. Heil*, 13 May 1983 (SJNM 2204). UTAH: San Juan Co. Ca. 0.5 mi north of Bluff on gravely hills, *K. Heil*, 12 August 1993 (SJNM 8087).

This species was among the first sclerocacti to be discovered and described. It grows on gravely and sandy hills, canyon rims and mesas at 5000–6000' (1500–1800 m) in desert and pinyon-juniper communities. It is often difficult to find because plants may grow in grama grass clumps, and the spines resemble the dried leaves of the grass.

Apparently *S. whipplei* does not hybridize in the wild with any other species. Near Agalatha Peak, Arizona, this taxon grows in close proximity to *S. parviflorus*; however, intermediate types have not been observed.

This species has been the object of considerable taxonomic confusion. Described in 1857 as *Echinocactus whipplei*, from near what is now Petrified Forest National Park, it was published simultaneously with *E. polyancistrus*. This was followed in 1863 by the description of *E. pubispinus* and *E. whipplei* var. *spinosior*, both from western Utah. In 1922, when Britton and Rose erected the genus *Sclerocactus*, they apparently misinterpreted the morphological features of the type of *S. whipplei*, confusing it with *S. spinosior*, *S. pubispinus*, *S. glaucus* and the then-unnamed *S. parviflorus* (note that these authors incorrectly described the flowers as purple). As specimens identifiable as *Sclerocactus* were accumulated (and in some cases deposited in herbaria) from northern Arizona, southern and eastern Utah, western Colorado and northwestern New Mexico, the natural tendency was to assign them to taxa previously described by Britton and Rose (e.g., Clover, 1938; Clover and Jotter, 1941). Much of the material was assigned to *E. whipplei*. As closer investigation revealed patterns of variation inconsistent with the material at the type locality and the type description of *E. whipplei*, new taxa were described. There has, however, been a tendency to align these taxa with *S. whipplei*. In 1966 Benson reduced many of the named taxa (i.e., *S. parviflorus*, *S. havasupaiensis* and varieties, and *S. intermedius*) to varietal status under *S. whipplei*. Castetter, Pierce and Schwerin (1976) continued with this practice by relegating the newly discovered taxa in New Mexico to *S. whipplei* as varieties *heilii* and *reevesii*. In his 1982 treatment of the cacti of the United States and Canada, Benson removed these taxa from under the *S. whipplei* umbrella, although some authors (Welsh, 1984; Welsh et al., 1994) have continued to maintain a very broad interpretation of *S. whipplei* to the extent that species such as *S. glaucus* are treated at the varietal level or only in synonymy under *S. whipplei*. Unfortunately, a broad interpretation of *S. whipplei* leads to the realization that (with the exception of *S. polyancistrus* and *S. mesae-verdae*) the entire genus *Sclerocactus* could be accommodated under *S. whipplei*. This may not be a problem if one has no concern for the evolutionary process (descent, with modification), localized morphological differentiation, regionalization and restriction of gene-flow, and historical perspectives (phylogeny) within *Sclerocactus*. If ease of pigeon-holing is the primary goal, then a broad species-concept (and the broader the better) is desired. We feel that a taxonomy should be based on an understanding of the evolutionary process and that taxonomies arbitrarily imposed on groups can only lead to confusion and misunderstanding of the taxa concerned and the process that produced their diversity. As a result we have followed the lead of Benson (1982) and Woodruff & Benson (1976) in restricting our concept of *S. whipplei* to the small, depressed-globose stemmed plants of the Little Colorado River drainage of Arizona, with flower buds that are broader than long, yellow tepals that expand in the afternoon (under bright light conditions) and flowers that are cylindric to narrowly funnelform in shape with the perianth bracts not spreading widely.

7. ***Sclerocactus cloveriae*** K. D. Heil & J. M. Porter, **nom. et stat. nov.**

S. whipplei (Engelm. & Bigelow) Britt. & Rose var. *heilii* Castetter, Pierce & Schwerin, Cact. Succ. J. (U.S.) 48:79. 1976.
Type. *Heil 3903A & B* (syntypes), northern San Juan County, New Mexico (UNM 49874; isotype, SJNM).

S. whipplei (Engelm. & Bigelow) Britt. & Rose var. *reevesii* Castetter, Pierce & Schwerin, Cact. Succ. J. (U.S.) 48:80. 1976.
Type. *Heil 4081*, southern San Juan County, New Mexico (UNM 51072; isotype, SJNM).

Figs. 4, 21.

Stems solitary, 2–3, green, elongate-cylindrical, ovoid when young, 3.9–25(–30) cm long (mean = 11.4 cm; SD = 4.3), 4.8–12.5(–15) cm in diam (mean = 8.4 cm; SD = 2.2); *ribs* usually 13, well-developed, the upper portion of the *tubercles* evident above the ribs, 5–14 mm long,

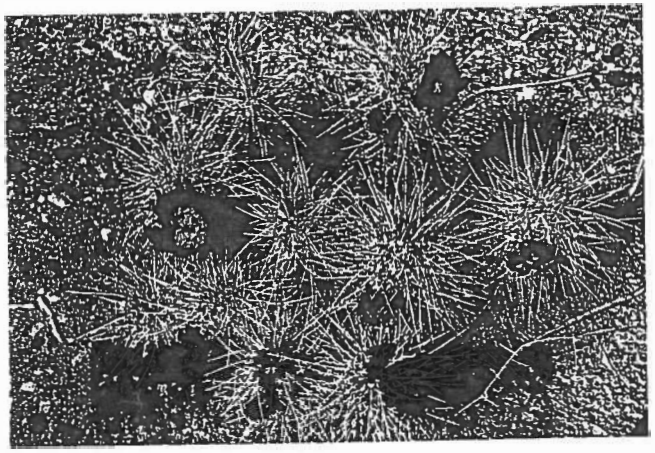


Fig. 4. *S. cloveriae*, Largo Canyon, San Juan, Co., New Mexico.

4.5–15 mm broad, protruding above the ribs 5–15 mm; areoles 4.5–8.5 mm diam, typically 9–24 mm apart; central *spines* 8 (6–9), the lower one straw-colored to brown, high-lighted with purple or red, terete or somewhat angled, hooked, porrect, (1.5–)3–4.6 cm long, ca. 1.5 mm wide, turned or curving somewhat downward, the lateral centrals 5–8, similar to the lower but a bit shorter and usually not hooked, the upper central white or straw-colored, straight or curved, angled to flat, somewhat inconspicuous, triangular in cross section, 2.5–5.5 cm long, 1–2 mm wide, erect; radial spines 4 (2–6), basally 1.3–2 mm wide, acicular, elliptic or rhombic in cross-section; *flower* 2.5–3.5(–4) cm long (mean = 3; SD = 0.26), 1.6–3.1(–3.6) cm in diam (mean = 2.3 cm; SD = 0.47), exterior floral tube glabrous, minutely papillate; *outer tepals* greenish to purple with brownish midribs, margins pink, purple or whitish, the larger oblanceolate, 10–18 mm long, 4–7.5 mm broad, mucronate, marginally membranous and crisped or minutely toothed; *inner tepals* purple, sometimes suffused with brown, the largest lanceolate, 15–22(–30) mm long (mean = 18.6; SD = 2.37), 4–6 mm wide at the broadest point (mean = 5.15; SD = 0.81), mucronate, somewhat irregularly toothed; *filaments* white, tinged with pink to pink-purple, 6–10 mm long, anthers yellow, 0.9–1.2 mm long, 0.3–0.5 mm wide; *style* tinged with pink or purple, rarely green, 14.6–19.5 mm long, 1–1.5 mm in diam, covered with minute but conspicuous papillae; stigma lobes 5–8, ca. 1.2–2.5 mm long, 0.5–1 mm broad; nectary chamber 1.5–2(–3) mm deep; ovary 3–7 mm long at anthesis; *fruit* green to tan, sometimes suffused with pink, dry, with a few membranous, scarious-margined, minutely toothed or fimbriate scales, 7–15 mm long, 5–12 mm broad, irregularly opening just below the middle or along a regular line of dehiscence at the base of the ovary; *seeds* brown or black, 1.9–3.5 mm diam, 1.2–2.5 mm long, hilum not deeply indented.

Distribution. Northwestern New Mexico north to southwestern Colorado. Scattered from south of Albuquerque, New Mexico, northward along the San Pedro and Rio Puerco River Valleys to near Waterflow and northward into southwestern Colorado along the Los Pinos, La Plata, and Animas rivers.

Holotype. The holotype is designated as *K. Heil 3903A*, northern San Juan County, New Mexico (UNM 49874).

Representative Specimens. COLORADO: La Plata Co. Valley of the La Plata, *T. S. Brandegee*, 1875 (GH). NEW MEXICO: San Juan Co. Blanco Mesa near Largo Canyon, *K. Heil*, 28 October 1978 (SJNM 2664). Rio Arriba Co. 1 mile northwest of Lybrook, *L. Benson*, 12 June 1965 (POM 317499). Sandoval Co. 2 mi south of San Ysidro, *Ken Heil*, 3 May 1986 (SJNM 6913). Valencia Co. 2 mi east of Laguna Pueblo on low hills, *Gil Wiens*, March 1970 (UNM 45296).

Recognition of *S. cloveriae* at the specific level is based in part on the lack of definitive characters to align it with other species of *Sclerocactus* with which it has been associated in the past. Originally designated as two weakly separable varieties of *S. whipplei* (Castetter, Pierce and Schwerin, 1976), the relationship of *S. cloveriae* to this species is far from unambiguous. Although *S. cloveriae* shares several features, i.e., flattened upper central spine, small flowers with perianth bracts that do not spread widely and flowers that lack granular papillae, these characters are not uniquely derived (unambiguously apomorphic) in *S. whipplei* and are therefore not evidence of relationship. Indeed, the floral ontogeny of *S. cloveriae* is not the same pattern as described in *S. whipplei* (Woodruff and Benson, 1976). The developmental patterns of the flowers are very similar to those found in *S. parviflorus*. It is not surprising that Benson, in his treatment of *Sclerocactus* (Benson, 1982) included *S. cloveriae* under *S. parviflorus* var. *intermedius*. A relationship between *S. cloveriae* and *S. parviflorus* might be further supported by the overall size of the plants. In general, both species are large-stemmed. Again it is not clear that stem-size represents unambiguous evidence of relationship, considering that large stems are also shared by *S. polyancistrus*. And though *S. cloveriae* and *S. parviflorus* appear to possess similar floral ontogenies, the distribution of that feature throughout *Sclerocactus* has not been documented. Moreover, *S. cloveriae* lacks large, granular papillae on the pericarpel (as found in *S. parviflorus*) and its flowers are significantly smaller than those of *S. parviflorus*. As a result of these conflicting morphologies, the phylogenetic affinities of *S. cloveriae* remain nebulous.

The specific epithet honors Elzada Clover, who conducted field studies of *Sclerocactus* on the southern Colorado Plateau in the late 1930's. We have chosen a novel epithet rather than selecting from existing varietal epithets in order to avoid any confusion. The two currently recognized varieties, *S. whipplei* var. *heilii* and *S. whipplei* var. *reevesii*, have no consistent morphological differences and should be considered one taxon. Also, because the circumscription is different than that implied by either of the type descriptions, we thought it appropriate, and within our right under the Code, to designate a new epithet.

7b. ***Sclerocactus cloveriae*** subsp. ***brackii*** K. D. Heil & J. M. Porter, **subsp. nov.**

Similis *Sclerocactus cloveriae* Heil & Porter in floribus sed in caulis brevioribus et spinis centralibus brevioribus differt.

Figs. 5, 14.

Stems 1(–2–3), green, elongate-cylindrical, ovoid when young, 2.9–7.5(–8.5) cm long (mean = 5.5 cm; SD = 1.39), 1.8–6.5(–7) cm in diam (mean = 5.2 cm; SD = 0.96); *ribs* usually 13, more or less obscure to well-developed, the upper portion of the *tubercles* evident above the ribs, 5–14 mm long, 4.5–15 mm broad and protruding above the ribs 5–15 mm; areoles 4.5–8.5 mm diam; central *spines* 4(–5), mostly four, the lower one often absent, but if present, straw-colored to brown, highlighted with purple or red, terete or somewhat angled, hooked, porrect, 0.7–3.1 cm long, ca. 1 mm in diam, turned or curving somewhat downward, the lateral centrals similar to the lower but a bit shorter and not hooked, 3 or 4, the upper central white or straw-colored, straight or curved, angled to flat, somewhat inconspicuous, triangular in cross section, 1.5–3.5 cm long, 1–1.5 mm broad, erect; radial spines 6–7 (5–8), basally 0.9–1.5 mm broad, acicular, elliptic or rhombic in cross-section; *flower* 2.3–3.5(–4) cm long (mean = 3 cm; SD = 0.37), 1.6–3 cm in diameter (mean = 2.5 cm; SD = 0.47), exterior floral tube glabrous, not minutely granular-papillate; *outer tepals* greenish to purple with brownish midribs, margins pink, purple, or whitish, the larger oblanceolate, 10–15 mm long, 3.5–7 mm broad, mucronate, marginally membranous and crisped or minutely toothed; *inner tepals* purple, sometimes suffused with brown, the largest lanceolate, 15–22(–30) mm long (mean = 19; SD = 0.20), 4–6 mm wide at the broadest point (mean = 4.75; SD = 0.09), mucronate, somewhat irregularly toothed; *filaments* white, tinged with pink to pink-purple, 6–10 mm long, anthers yellow, 0.9–1.2 mm long, 0.3–0.5 mm wide; *style* tinged with pink or purple, rarely green, 14.6–19.5 mm long, 1–1.5 mm in diam, covered with minute but conspicuous hairs; stigma-lobes 5–8, ca. 1.2–2.5 mm long, 0.5–1 mm broad; nectary chamber 1.5–2(–3) mm deep; ovary 3–7 mm long at anthesis; *fruit* green to tan, sometimes suffused with pink, dry, with a few membranous, scarious-margined, minutely toothed or fimbriate scales, 7–15 mm long, 5–12 mm broad, irregularly opening just below the middle or along a regular line of dehiscence at the base of the ovary; *seeds* 1.9–3 mm long, 1.2–2 mm broad, hilum not deeply indented.

Holotype. *K. Heil #8149*; sandy clay hills on the Nacimiento Formation, Kutz Canyon, San Juan County, New Mexico (SJNM 2695).

Habitat. Sandy clay soils of the Nacimiento Formation, associated with *Eriogonum shockleyi*, *Gilia formosa*, and *Swertia utahensis* at 5000–6000' (1500–1800 m).

Distribution. Endemic to San Juan County, New Mexico, occurring in scattered populations along a small portion of the San Juan River Valley near Bloomfield. The subspecies extends north to near Aztec and south to near Dzith-Na-O-Dithle.

This subspecies was first discovered in the mid 1960's by Bob Reeves. These populations represent an interesting but common pattern of morphological divergence in *Sclerocactus*. As has been documented in many animals (e.g., Alberch and Alberch, 1981) and occasionally in plants (Guerrant, 1982; Lord and Hill, 1987), shifts in developmental rates with respect to the onset of sexual maturation has been a recurring theme in the evolution of morphological novelty. Such shifts in rates of development or heterochrony (Gould, 1977; Alberch et al., 1979) of organisms may come about in several ways. The rate itself may change. If the rate increases, the mature morphology is reached more quickly relative to

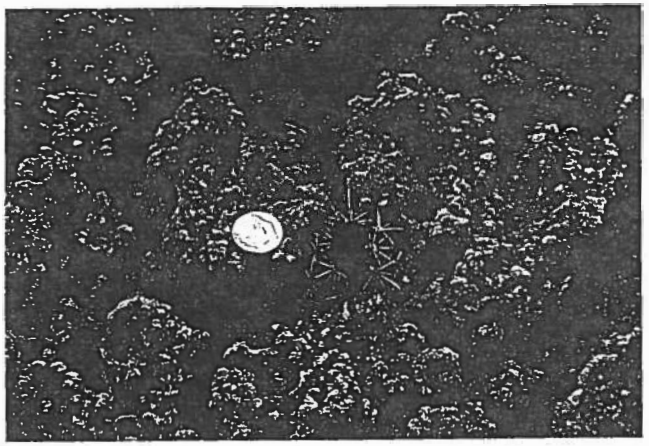


Fig. 5. *S. cloveriae* subsp. *brackii* in bloom, San Juan Co., New Mexico.

the ancestral developmental pattern. If the rate decreases relative to the ancestral ontogeny, then it takes a greater amount of time to attain the mature morphology. Alternatively, the rate of development of the organism may stay the same but the timing of the appearance of some feature of interest (e.g., sexual reproduction) may change. The timing may be delayed or moved forward. In the case of *S. cloveriae* subsp. *brackii*, the timing of flowering has been moved forward so that an immature stem (by comparison to *S. cloveriae* subsp. *cloveriae*) is sexually mature. Such a hypothesis assumes that the ancestral development pattern is like that of subsp. *cloveriae*. There is some support for this assumption, based on a preliminary cladistic analysis of *Sclerocactus* (Porter and Heil, unpubl.).

The distinction between subspecies *brackii* and *cloveriae* is striking when subsp. *brackii* begins sexual reproduction. Its stem is generally 3 cm or less in diameter (often about 2 cm) when flowers are first produced. This contrasts with the stems of subsp. *cloveriae*, which, on average, are 11.4 cm long and 8.4 cm in diameter. At this early stage in stem development, adult-phase areoles have not formed and juvenile spine arrangements are common. The juvenile spine arrangements are marked by five to seven short, white, radial spines (generally only four are found in subsp. *cloveriae*) and mostly four short central spines, one or none of them hooked (subsp. *cloveriae* usually has eight central spines, one of which is hooked). However, as subsp. *brackii* matures, the morphologies of the two varieties tend to be more convergent, both in stem and spine features.

This subspecies is named in honor of Steven Brack, who has conducted numerous field studies of *Sclerocactus*; he is owner of Mesa Gardens in Belen, New Mexico.

8. ***Sclerocactus pubispinus*** (Engelm.) L. Benson

Echinocactus pubispinus Engelm., Trans. Acad. Sci. St. Louis 2:199. 1863. *S. pubispinus* (Engelm.) L. Benson, Cact. & Succ. J. (U.S.) 38:103. 1966. *Pediocactus pubispinus* Arp, Cact. Succ. J. (U.S.) 44:222. 1972.

Type. *Engelmann s.n.*, Pleasant Valley, near Salt Lake Desert, according to Benson, 1982. =Goshute Range, White Pine County, Nevada (MO).

Figs. 6, 15.

Stems solitary (–2–3), green, depressed-hemispheric to ovoid, or cylindric, 2–15 cm diam, 1–15 cm long, *ribs* usually 13, the upper portion of the *tubercles* prominent above the ribs, 6–17 mm long, 5–17 mm broad; areoles 3–6 mm broad; spines dense but not obscuring the stem, those of juvenile plants, and sometimes others, densely or sparingly white-pubescent, later glabrous; central spines 4 (0–6), the single lower central tan to brown, reddish or black, often hooked, 1–5.5 cm long, lateral spines 2–4 (0–6), white, tan, red or reddish-brown, sometimes hooked, mostly 1–2 cm long, the upper one white or dark-tipped, flattened, 0.5–6 cm long, 0.7–2.2 cm wide; radial spines white or with dark tips, 8–11 (6–16), spreading, mostly 5–35 mm long, 0.3–1 mm diam; *flower* 2–4 cm long and in diam; *outer tepals* with pink to yellowish-brown, greenish-brown, or reddish-brown midribs and cream to yellow or pink to reddish-purple margins, mostly oblanceolate, 1–2 cm long, 4–8 mm broad; *inner tepals* cream with yellow to greenish or with reddish-purple to red violet or lavender or brownish centers and lighter margins, mostly oblanceolate, 1.5–2.5 cm long, 4–7.5 mm broad; *filaments* cream to yellow, green, or red-violet to pink, 6–12 mm long, anthers yellow, 1–1.5 mm long; *style* mostly pink to reddish-violet; stigma lobes 5–9(–10), ca 1.5–2 mm long, green to yellow; *fruit* green to pink, dry, barrel-shaped, with a few membranous slightly-scarious-margined, scales, (9–)10(–12) mm long and thick, splitting along 2–4 vertical slits; *seeds* black, 2–2.5 mm long, 3–4 mm broad, 1–2 mm thick.

Distribution. Western Utah and the northeastern edge of Nevada.

Representative Specimens. NEVADA: Elko Co. 6.5 mi S of Pilot Peaks, *R. Foster*, 25 May 1979 (BRY 199701). White Pine Co. Pleasant Valley, ca. ⅛ mi W of the Utah-Nevada State line, *B. F. Harrison & K. Thorne*, 13 June 1979 (BRY 202061). UTAH: Beaver Co. Hamlin Valley, ca. 1.25 mi S of Millard Co. line, *S. L. Welsh, and M. Chatterley*, 2 June 1980 (BRY 211220). Box Elder Co. Mountains, *E. F. Wiegand*, 8 August 1954 (POM 284745). Iron Co. Beryl Desert, *C. Lambert*, 9 July 1939 (BRY 004). Juab Co. Deep Creek Mountains, ca. 0.5 mi E of Nubold Ranch, *S. Welsh, R. Foster, and J. Henriod*, 6 June 1978 (BRY 184086). Millard Co. West side of the Wah Wah Mountains, *K. Heil*, 15 May 1983 (SJNM 2202). Tooele Co. Silver Island Mountain Range northeast of Wendover, *L. H. Bowker*, 1969 (POM 317897).

Sclerocactus pubispinus grows on light-colored soils of limestone or dolostone origin and is very difficult to locate in the field. It is mostly at 6000–6800' (1800–2000 m) growing with sagebrush, saltscale, pinyon, and juniper. Benson (1982) recognized *S. pubispinus* and *S. spinosior* at the species level while S. Welsh et al. (1987) treats them as two varieties of *S. pubispinus*. There seems little question that these two species, along with *S. blainei* and probably *S. sileri*, form an alliance of related taxa. The Wah Wah Mountains and Confusion Range appear to act as barriers to genetic exchange between these two taxa; however, in the few locations where the two taxa meet there seems to be hybridization. We treat these taxa at the specific level largely to maintain a consistant treatment across the genus.

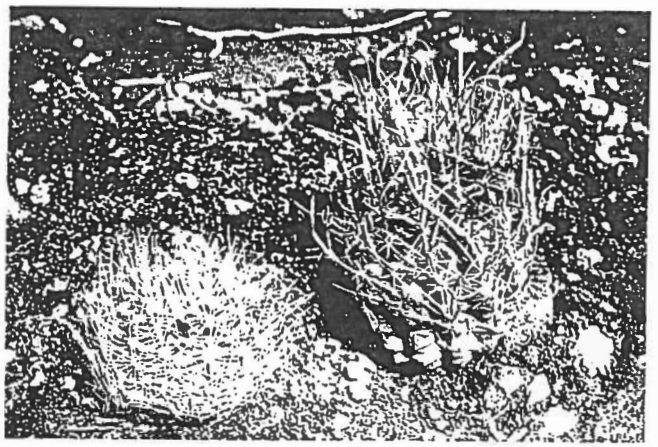


Fig. 6. Stems of *S. pubispinus* (left) and *S. blainei*.

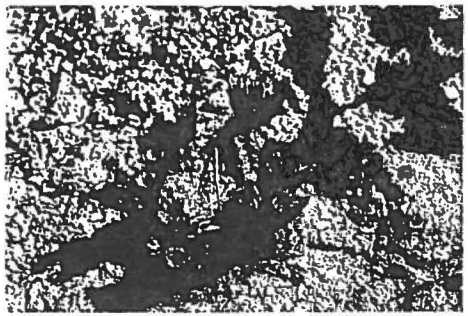
9. ***Sclerocactus spinosior*** (Engelm.) Woodruff & Benson, Cact. Succ. J. (U.S.) 48:133. 1976.

Echinocactus whipplei Engelm. & Bigelow var. *spinosior* Engelm., Trans Acad. Sci. St. Louis 2:199. 1863. *E. spinosior* Hirscht, Monatsschr. Kakteenk. 11:89. 1901. *E. spinosior* Brandegee ex Britt. & Rose, Cactaceae 3:213. 1922 (Benson, 1982, notes that the citation in B.&R., "Hirscht ex Purpus, Monatsschr. Kakteenk. 10:119. 1900", is incorrect). *E. whipplei* Englem. & Bigelow f. *spinosior* Schelle, Handb. Kakteenkultur 158. 1907. *Sclerocactus whipplei* (Engelm. & Bigelow) Britt. & Rose var. *spinosior* Engelm. ex Boissevain & Davidson, Colorado Cacti, 51–52. 1940. *S. spinosior* (Engelm.) D. Woodruff & L. Benson, Cact. Succ. J. (U.S.) 48:131. 1976. *S. pubispinus* (Engelm.) L. Benson var. *spinosior* (Engelm.) S. L. Welsh, Great Basin Naturalist 44:52–69. 1984.

Type. *Engelmann s.n.*, 29 July 1859, Desert Valley, west of Camp Floyd, Utah (MO, lectotype, consisting of flowers and seeds).

Fig. 16, cover.

Stem depressed globose to ovoid, mostly solitary, 4–15 cm long, 4.5–10 cm diam; *ribs* 13–14, tuberculate; *tubercles* one-fourth to one-half as high as rib beneath, 6–17 mm long, 6–15 mm broad; *areoles* circular to elliptic, 3–6 mm broad, 6–12 mm apart; *spines* rather dense, those of juvenile plants densely white-pubescent; central spines white on juvenile stems and therefore on older (lower) parts of mature stems, the lower centrals of upper areoles 3, tan to brown, reddish to black, the upper central spines 4–6, the principal lower spines 1–2, mostly hooked, 2–3 cm



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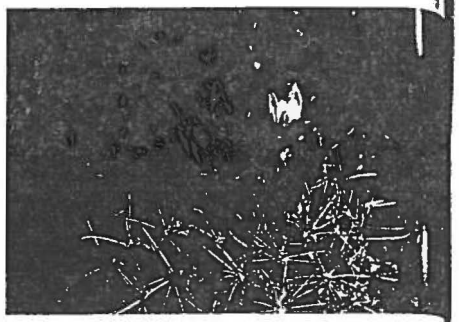

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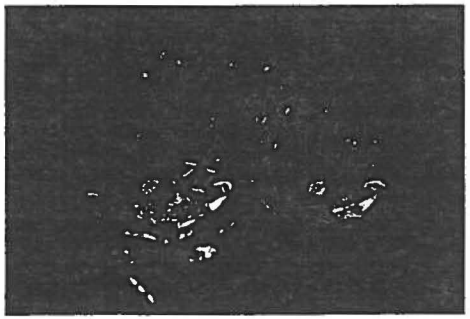

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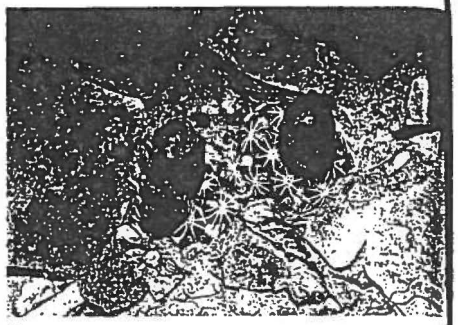

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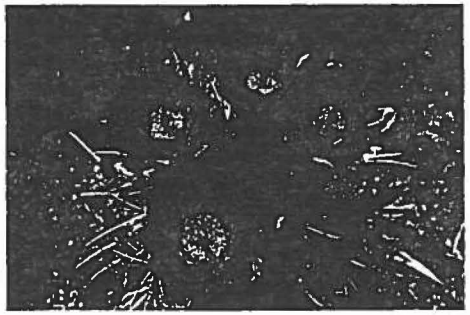

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Fig. 7. *S. mesae-verdae* with pink flowers. South of Shiprock, San Juan Co., New Mexico.
Fig. 8. *S. wrightiae* with cream flowers. Cathedral Valley, Capitol Reef National Park, Utah.
Fig. 9. *S. glaucus* north of Debeque, Garfield, Co., Colorado.
Fig. 10. *S. brevispinus* in bloom. Note the lack of—or extremely small—central spines. Duchesne Co., Utah.
Fig. 11. *S. parviflorus* subsp. *parviflorus*. Canyonlands National Park, San Juan Co., Utah.
Fig. 12. *S. parviflorus* subsp. *intermedius* in full bloom near the Goosenecks of the San Juan River, San Juan Co., Utah.

long, basally 1–1.2 mm broad, lateral centrals 2, the upper central white, flat, 2–6 cm long, up to 1.5 mm broad; radial spines white, 6–10, spreading, the longer mostly 1–3.5 cm long, *flower* 2–4 cm diam and long; *outer tepals* with greenish-brown or reddish-brown midribs and pinkish margins, oblanceolate, mostly 1–2 cm long, 4.5–7 mm broad, nearly entire; *inner tepals* reddish-purple to violet or lavender, narrowly oblanceolate, mostly 2.5 cm long, 6–8 mm broad, nearly entire; *filaments* red-violet to pink, green, or yellow; anthers yellow, 1–1.5 mm long; style mostly pink to reddish-violet, 1.5–2 cm long, stigmas 5–10; *fruit* green and turning reddish at maturity, with up to 2 scales, barrel-shaped, 9–12 mm long and in diam, opening along 2–4 vertical slits; *seeds* 2–2.5 mm long, 3–4 mm broad, 1.5–2 mm thick (Benson, 1982).

Distribution. Southwestern Utah.

Representative Specimens. UTAH: Beaver Co. Pine Valley, south of Sewing Machine Pass, *S. L. Welsh & M. Chatterley,* 29 June 1980 (BRY 212559). Iron Co. Antelope Ranch near mile marker 33 on State 56, *K. Heil,* 17 May 1983 (SJNM 2198). Emery Co. 0.8 mi due east of Sevier Co. Line, 2 mi south of I-70, *E. Neese, S. Welsh, S. White,* 15 June 1979 (BRY 198724). Millard Co. Adjacent to Lawson Cove, Wah Wah Valley, *S. L. Welsh, M. Chatterley,* 25 June 1980 (BRY 212470). Juab Co. Thomas Pass, *L. & E. Benson,* 20 April 1963 (POM 306828). Sevier Co. Joseph City, *K. Heil,* May 1980 (SJNM 2630).

This species has a long history of confusion. The type specimen is of such poor quality that, were it not for knowledge of the collection locality, it could belong to nearly any sclerocactus. Moreover, there has been a long-standing confusion between *S. spinosior* and *S. parviflorus.* This confusion dates back at least to Coulter's treatment of *Echinocactus* (1896:368): "As far as known, *E. whipplei* is confined to the region of its original discovery (valley of the Little Colorado, northern Arizona), and *spinosior* to the deserts of southern Utah and southwestern Colorado, a considerable distance to the north." This usage persisted in the literature (see Boissevain and Davidson, 1940) until Benson's treatment (1966a, b). Current interpretation is based on modern collections from the vicinity of the type because, as mentioned above, the holotype consists only of flowers and seeds.

Sclerocactus spinosior is found east of the Wah Wah Mountains and Confusion Range and extends east to the Colorado Plateau. It grows on igneous or calcareous gravels and is usually associated with pinyon-juniper woodland, shadscale, or sagebrush communities at 5000–6600' (1525–2000 m).

10. ***Sclerocactus blainei*** Welsh & Thorne, Great Basin Naturalist, 45:553–555. 1985.

S. blainei S. L. Welsh & K. Thorne, Great Basin Nat. 45:553. 1985.
Type. *S. L. Welsh,* 1.6 mi northeast of Currant, Nye County, Nevada (BRY).

S. schlesseri K. Heil & S. L. Welsh, Great Basin Nat. 46:677. 1986.
Type. *K. Heil s.n.,* Lincoln County, Nevada, Tertiary lacustrine deposits, ca. 1464 m (BRY; Isotype, NY).

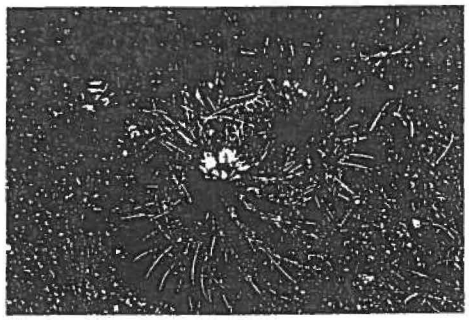
Figs. 6, 17.

Stems dark green, solitary or colonial, ellipsoid, obovoid, ovoid to cylindric, 3–15 cm tall, 4–6(–8) cm wide; *ribs* 6–13; *tubercles* 12–18 mm wide, 8–10 mm long; areoles woolly, finally glabrate; *spines* flexible, densely pubescent when young; upper central spine 1, ascending, flat to trigonous, ribbonlike, curved, cartilaginous to bony, pubescent to glabrous, 3–5.5 cm long, 1–2.5 mm wide, reddish brown to white; peripheral central spines 2, ascending, flat, ribbonlike, sometimes hooked, pubescent, 2–3 cm long, 0.5–1 mm wide, black to white; lower central spine 1, ascending, flexible, irregularly hooked, pubescent, 2.5–4.5 cm long, to 1 mm wide, black, gray, tan, or white; radial spines 6–9 (–12), flattened, flexible, pubescent, 3–14 mm long, white; *flowers* apical on upper end of the tubercles near the top of the areoles and above the spines, funnelform, 3–4 cm long, 2–3 cm wide, violet pink; *outer tepals* oblanceolate, finely irregularly toothed apically, mucronate, violet pink with brownish midstripes, 1.5–2 cm long, 6–10 mm wide; *inner tepals* oblanceolate, entire or slightly undulate, minutely toothed apically, violet pink, 1.5–2 cm long, 4–5 mm wide, *filaments* red, anthers yellow; stigma lobes 7–9, light green; *fruit* dry, barrel-shaped, naked or with one or two scales, 1–1.5 cm long, 9–13 mm wide, red to greenish red, dehiscing by a transverse break in the ovary wall, the perianth persistent; *seeds* 2 mm long, 3 mm wide, ca. 1 mm thick, pyriform with slightly flattened apex, shiny black, papillate, becoming less so near the hilum; hilum elliptic, 1 mm wide (Heil and Welsh, 1986; Welsh and Thorne, 1985).

Distribution. Iron County, Utah, and Nye and Lincoln counties, Nevada.

Representative Specimens. NEVADA: Lincoln Co. Cathedral Gorge State Park near Panoca, *K. Heil & D. Schleser,* 16 May 1983 (SJNM 2205). Nye Co. 1 mi northeast of Currant, *S. L. Welsh,* 23 May 1981 (BRY 224612). UTAH: Iron Co. Lund, *J. Busek,* April 1980 (SJNM 2632).

This is a peculiar series of populations related to *Sclerocactus spinosior* and *S. pubispinus.* The flower size is larger and the upper central spine is longer than in either *pubispinus* or *spinosior.* The central spine number varies, and the number of hooked spines may number six, which is characteristic of *S. polyancistrus.* However, we feel this taxon shares more characteristics with *S. spinosior* than with *S. polyancistrus.* The distinction between *S. schlesseri* and *S. blainei* rests



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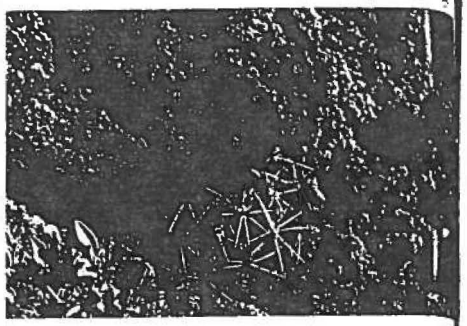

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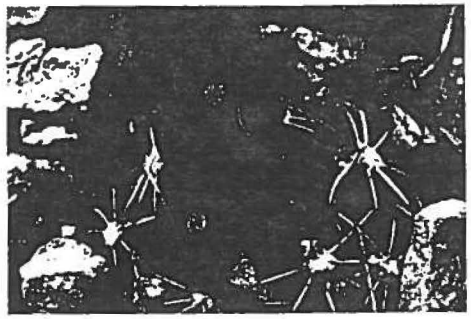

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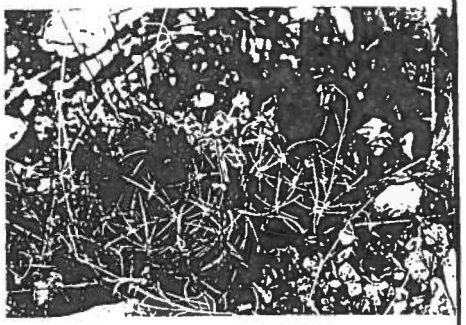

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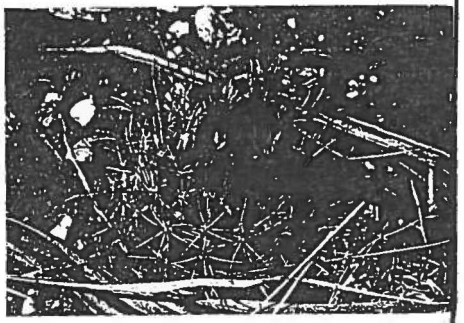

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Fig. 13. *S. parviflorus* subsp. *terrae-canyonae* with typical yellow flowers. Natural Bridges National Monument, San Juan Co., Utah.
Fig. 14. *S. cloveriae* subsp. *brackii* in full bloom. Note the lack of central spines in some of the areoles. San Juan Co., New Mexico.
Fig. 15. *S. pubispinus* in bloom near the Desert Range Experimental Farm, Millard Co., Utah.
Fig. 16. *S. spinosior* near Joseph, Sevier Co., Utah.
Fig. 17. *S. blainei* in flower, Cathedral Valley, Lincoln Co., Nevada.
Fig. 18. *S. sileri* with light yellow flowers, Houserock Valley, Coconino Co., Arizona.

largely in stem shape. *S. schlesseri* has a much narrower stem, but this seems scarcely enough difference to warrant taxonomic status. *S. blainei* is found in greasewood, galleta grass, shadscale, and sagebrush communities at 4900–5400′ (1464–1830 m) on limestone and igneous gravel substrates.

11. **Sclerocactus sileri** (L. Benson) K. D. Heil & J. M. Porter, **nom. et stat. nov.**

S. pubispinus (Engelm.) D. Woodruff & L. Benson var. *sileri* L. Benson, Cacti of Arizona, ed. 3. 23, 179. 1969.
Type. *P. H. Siler s.n.* (F). 1888. Southern Utah; Isotype (US).

Fig. 18.

Stems 1 (–2), green, depressed globose, up to 5.5 cm long, 3.5–5.5 cm in diam; *ribs* usually 13, not well-developed, *tubercles* 7–12 mm long, 6–15 mm broad and protruding above the ribs; areoles 3–4 mm diam, typically 12–15 mm apart; central *spines* 4, the lower white, gray or purplish tinged, angled, strongly hooked, slightly contorted, 1.2–3 cm long, 0.5–1 mm wide, turned or curving somewhat downward, the lateral centrals 2, similar to the lower but a bit shorter, and usually not hooked, the upper central white to tan, recurved, strongly flattened, conspicuous, 1.3–3 cm long, 0.75–2 mm wide, erect; radial spines 6–8, basally 0.5–0.75 mm wide, acicular, elliptic in cross-section; *flower* 2.5–3 cm long, 2–3 cm in diam, exterior floral tube glabrous; *outer tepals* with brownish and yellowish margins, the larger oblanceolate, 10–15 mm long, 5–8 mm broad, mucronate, marginally membranous and crisped or minutely toothed; *inner tepals* yellow, sometimes suffused with brown, the largest lanceolate, 15–25 mm long, 5–7 mm at the broadest point, mucronate; *filaments* white, 7–10 mm long, anthers yellow, ca. 1 mm long, 0.3–0.5 mm wide; *style* yellowish-green, 14–20 mm long, 1–1.5 mm in diam; stigma lobes 5–8 ca. 1.2–2.5 mm long, 0.5–1 mm broad, nectary chamber 1.5–3 mm deep; ovary 3–7 mm long at anthesis; *fruit* green, turning red, ovoid, dry, with a few membranous scarious-margined, minutely toothed or fimbriate scales, 0.8–2.2 cm long, 0.8–1.4 cm broad, opening along two to four vertical slits; *seeds* black, 2.75–3 mm diam, 2.25–2.5 mm long.

Distribution. Coconino County, Arizona, and Clark County, Nevada.

Representative Specimens. ARIZONA: Coconino Co. Ca. 4.3 mi north of Alt. 89, up House Rock Valley, *K. Heil,* 13 May 1986 (SJNM 6946). Paria Plateau, T40N, R4E, S20, *R. Gierisch,* 25 June 1987 (ASC).

This is an unusual little cactus with characteristics similar to both *Sclerocactus whipplei* and *S. spinosior.* The spination and flower color is reminiscent of *S. whipplei*; however, the fruit dehisces (by 2–4 longitudinal slits) as in *S. spinosior.*

J. Busek (1983) applies the name *S. pubispinus* var. *sileri* to those cacti in southwestern Utah and Nevada; however, *S. pubispinus, S. spinosior,* and *S. blainei* of the Great Basin are not the same species as *S. sileri,* which is found on the Arizona strip.

This cactus is very difficult to locate in the field, which is probably for the best, as it appears to be quite rare and potentially in need of protection. It often occurs in grama grass, associated with drop seed, yucca, hedgehog cactus, sagebrush, snakeweed, pinyon, and juniper.

12. ***Sclerocactus polyancistrus*** (Engelm. & Bigelow) Britt. & Rose, Cactaceae 3:213. 1922.

Echinocactus polyancistrus Englem. & Bigelow, Proc. Amer. Acad. 3:272. 1857. *Pediocactus polyancistrus* (Engelm. & Bigelow) Arp, Cact. Succ. J. (U.S.) 44:222. 1972.
Type. *Bigelow s.n.*, head of the Mojave, 15 March 1854 (MO).

Hermit Cactus (Fig. 20)

Stems solitary or in clusters, cylindroidal or elongate-cylindroidal, 10–40 cm long, 5–9 cm in diam; *ribs* well-developed, 13–17; *tubercles* ca. 12 mm long, 10 mm broad; areoles elliptic, mostly 9 mm apart; spines dense and obscuring the stem; central *spines* 9–11, the 6–8 lower and lateral central spines red or reddish-brown, rarely yellow, 3–4.6 cm long, 1 mm wide, mostly hooked, upper central spines mostly 3, white, flat, mostly 3.7–8.6 cm long, 1.5–3 mm wide, mostly hooked; radial spines white, 10–18, 5–6 cm long, flat, straight; *flower* ca. 5 cm diam, 5–6 cm long, with a spicy, pungent odor; *outer tepals* with greenish-purple midribs and rose-purple or magenta margins, cuneate-spathulate, mostly 25 mm long, 6–9 mm broad; *inner tepals* rose purple to magenta, the largest ovate-lanceolate, 24–40 mm long, 9–12 mm broad; *filaments* greenish-yellow, 6–12 mm long; anthers cream-colored, nearly 2 mm long, 1 mm broad; *style* green to cream, mostly 2.5 cm long, 1.5 mm diam, smooth, with 8–10 grooves; stigmas pink, mostly 10; ovary at maturity with a few white scales; *fruit* green to tan, dry at maturity, barrel-shaped, 2.2–3 cm long, 1.2–2.1 cm diam; *seeds* shiny black, 3 mm diam, 2 mm long, 1 mm thick, finely papillate.

Distribution. Mojave Desert of California; Esmeralda and Nye Counties in Nevada.

Representative Specimens. CALIFORNIA: Inyo Co. Red Rock Canyon, *H. Rush,* 15 May 1948 (POM 432261). Kern Co. Redrock Canyon, *L. Benson,* 24 April 1932 (POM 273961). San Bernardino Co. One mile south of Oro Grande, *L. Benson,* 11 May 1968 (POM 317492). NEVADA: Esmeralda Co. Near Pinyon Hill, White Mountains, *V. Duran,* 17 June 1930 (POM

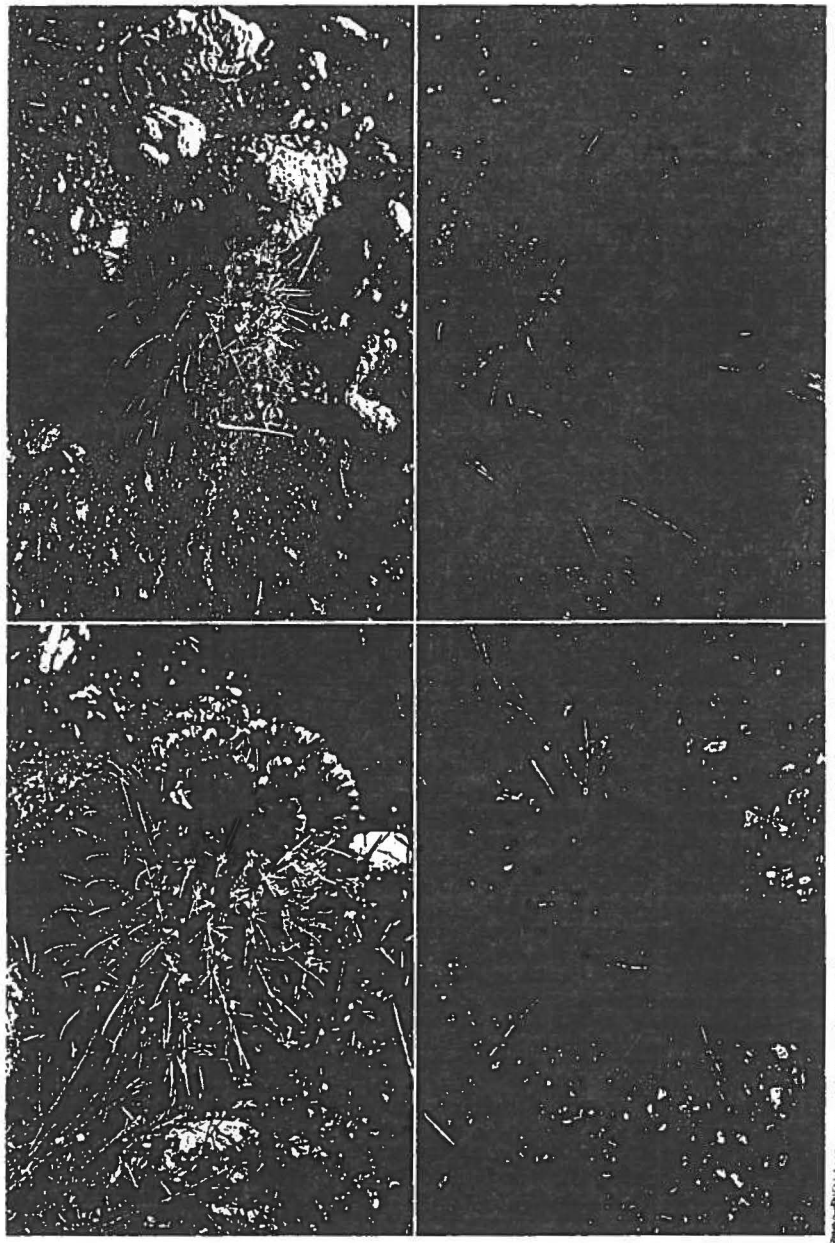

Fig. 19 (upper left). *S. wrightiae* with pink flowers. Cathedral Valley, Capitol Reef National Park, Utah.
Fig. 20 (upper right). *S. polyancistrus* with garnet-colored flowers, near Goldfield, Nevada.
Fig. 21 (lower left). *S. cloveriae,* Farmington, San Juan Co., New Mexico.
Fig. 22 (lower right). *S. nyensis* growing in volcanic tuff near Tonopah, Nevada. Photos: Figs. 5 and 18 by Dave Schleser; all others by Ken Heil.

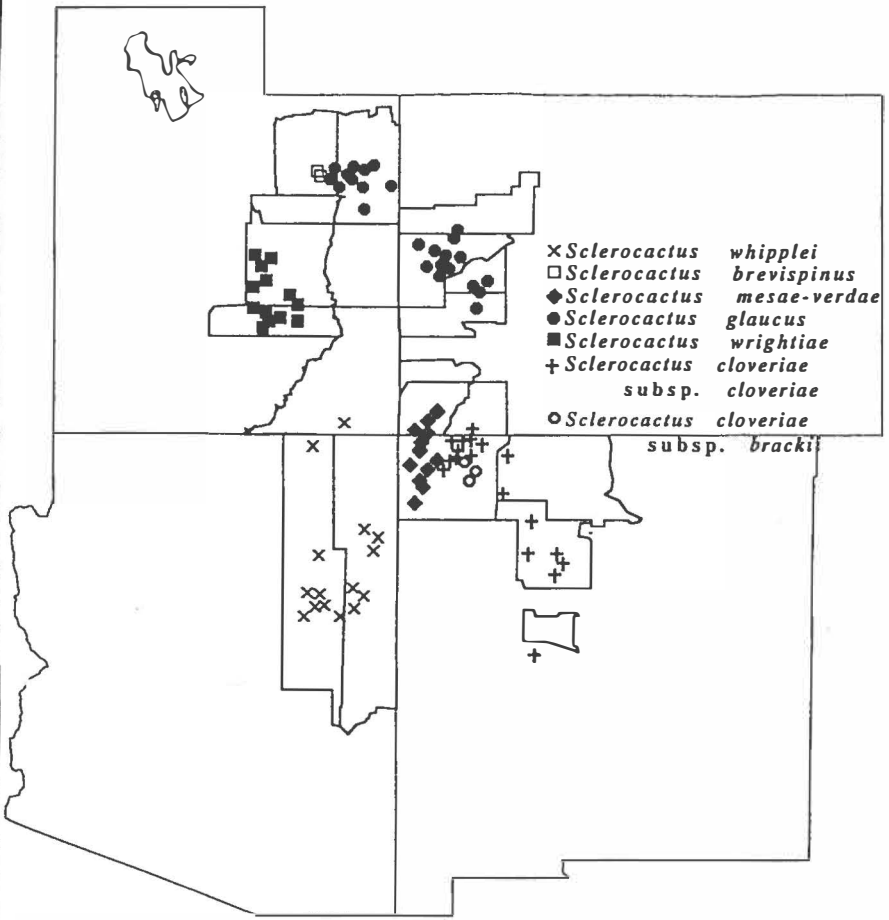

Fig. 23. Distribution of six species of *Sclerocactus* in Arizona, Colorado, New Mexico and Utah based on herbarium collections.

219826). Nye Co. Ca. 12 mi east of Tonopah, Toiyabe National Forest, *K. Heil,* 16 May 1986 (SJNM 6935).

Sclerocactus polyancistrus grows on rocky soils in the Mojave Desert at 2500–7000' (750–2100 m). This species, the type of the genus, is a particularly unusual member of *Sclerocactus.* It is the only member of the genus that lacks papillae on the style, and its style possesses grooves, somewhat reminiscent of those in *Ferocactus. S. polyancistrus* is also the largest species, grows the furthest west, produces the largest flowers and longest spines, and is found at the lowest elevation. *S. polyancistrus* and *S. nyensis* are the only representatives of sclerocacti found in the Mojave Desert.

The contrasting red and white spines, and large flowers make this one of the most attractive of the *Sclerocactus* species.

13. ***Sclerocactus nyensis*** Hochstätter, Succulenta 71(6):247–262. 1992.
Type. *F. Hochstätter, 105*; West Nye County, Nevada (HBG).

Fig. 22.

Stems solitary, or 2–3, globose, cylindroidal or elongate-cylindroidal, 5–12 cm long, 4–5 cm in diam; *ribs* well-developed, 12–15; *tubercles* 10–12 mm long, 10 mm broad; areoles elliptic, mostly 13 mm apart; spines dense and obscuring the stem; central *spines* 4–7, the 3–5 lower and lateral

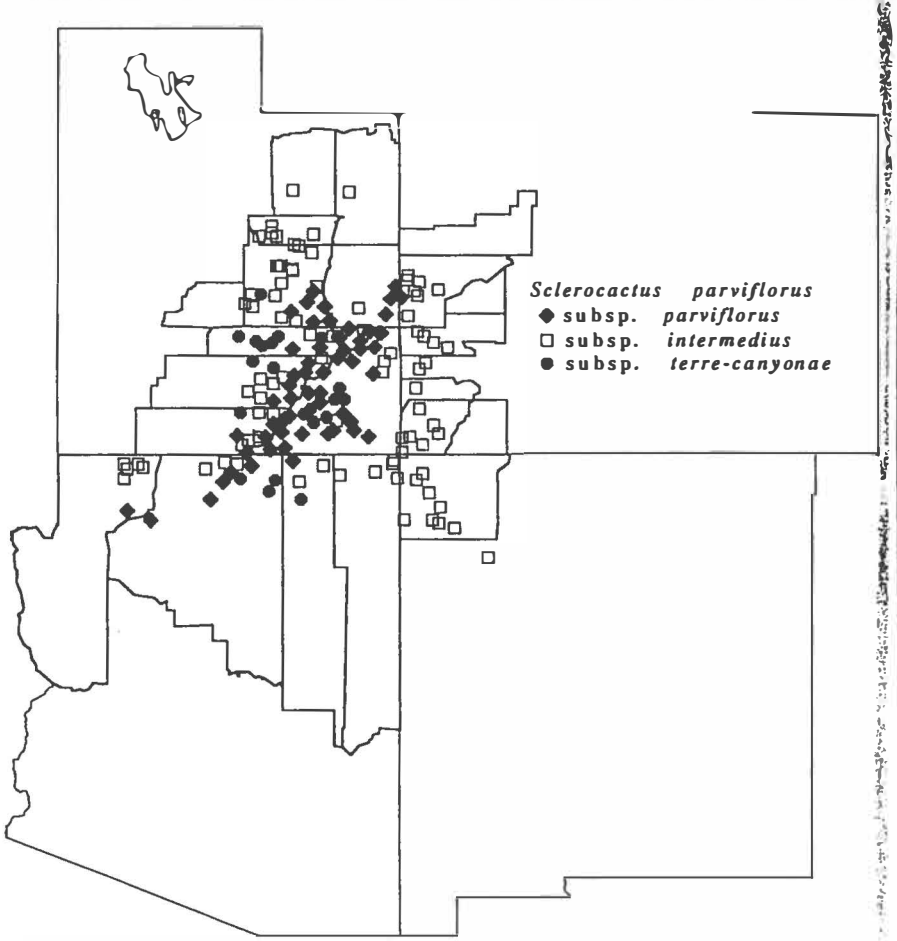

Fig. 24. Distribution of three subspecies of *S. parviflorus* in Arizona, Colorado, New Mexico and Utah based on herbarium collections.

central spines red or reddish-brown, 2–3.6 cm long, 0.75 mm wide, mostly hooked, upper central spines mostly 1–2, white, flat, mostly 2.5–4.5 cm long, 1.5–2 mm wide, rarely hooked; radial spines white, 12–17, 8–12 mm long, flat, straight; *flower* ca. 2–2.5 cm diam, 3–4 cm long; *outer tepals* with greenish-purple midribs and rose-purple or magenta margins, cuneate-spathulate, mostly 10–17 mm long, 5–8 mm broad; *inner tepals* rose purple to magenta, the largest ovate-lanceolate, 18–22 mm long, 6–8 mm broad; *filaments* green, 6–12 mm long, anthers cream to yellow, nearly 1 mm long, 0.5 mm broad; *style* green, mostly 2 cm long, 1 mm diam; stigmas green, mostly 10; ovary at maturity with a few white scales; *fruit* green to tan, dry at maturity, barrel-shaped, 1.5–2 cm long, 0.75–1.5 cm diam; *seeds* shiny black, 3 mm long, 2 mm wide, 1 mm thick, irregularly furrowed.

Distribution. Esmeralda and Nye counties, Nevada.

Representative Specimens. NEVADA: Esmeralda Co. Ca. 3 mi south of Tonopah, 1.3 mi south of old highway entrance on both sides of U.S. 95, *Heil & Porter,* 15 May 1986 (SJNM 6958). Nye Co. 10 mi south of Warm Springs, *K. Heil,* 16 May 1983 (SJNM 2773).

Sclerocactus nyensis has the appearance of a dwarf *S. polyancistrus*; however, the seeds differ slightly from other sclerocacti. *S. nyensis* possesses seeds that are furrowed or grooved, much as in a prune. This species is very likely another paedomorphic derivative. It has many of the characteristics shared by other presumed paedomorphs: globose stems, increased frequency of reproductive plants lacking central spines, and short, more or less barrel-shaped flowers.

S. nyensis was first discovered by Richard May in the early 1980's, growing on volcanic tuff and other volcanic deposits near Warm Springs and south of Tonopah at an elevation of approximately 5250–5700'. This cactus is usually found in full sunlight, but a few were found growing under desert shrubs. It blooms in mid-May.

There has been a considerable amount of confusion with the nomenclature of *S. blainei, S. schlesseri,* and *S. nyensis. S. schlesseri* was originally described in 1986 by Heil and Welsh, with

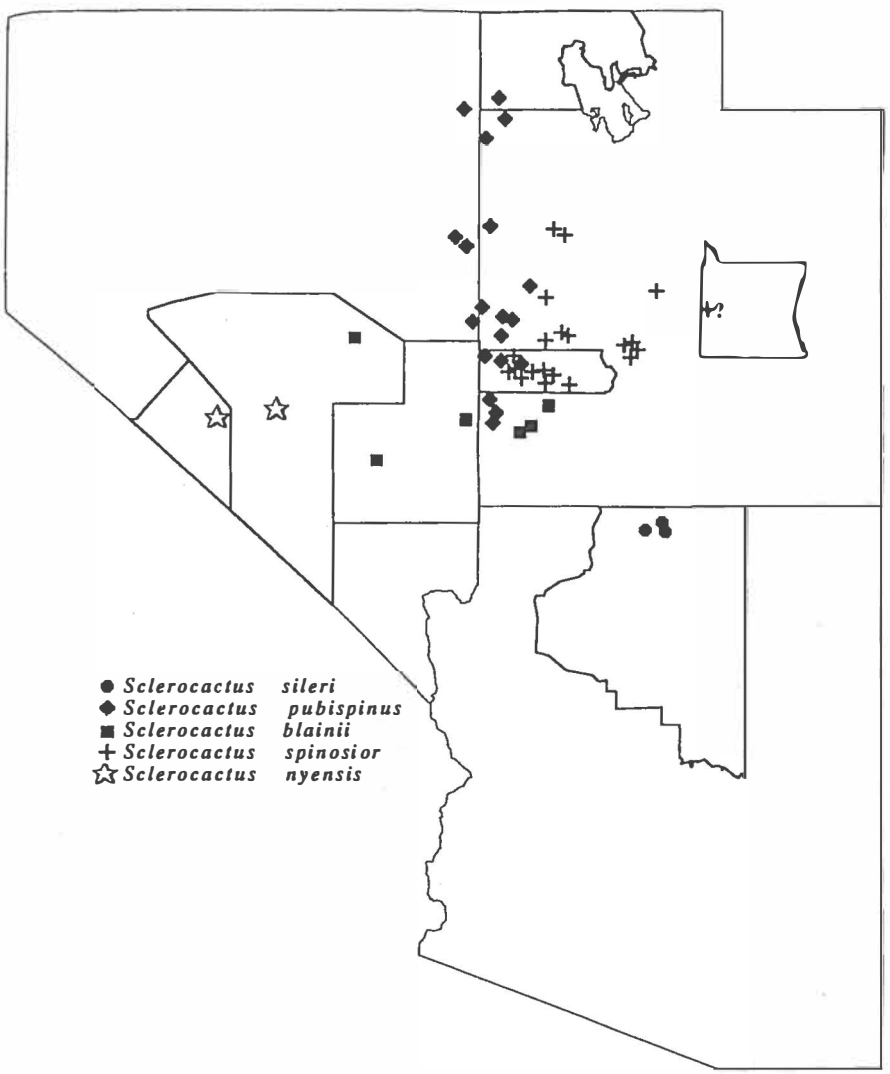

Fig. 25. Distribution of five species of *Sclerocactus* in Arizona, Nevada and Utah based on herbarium collections.

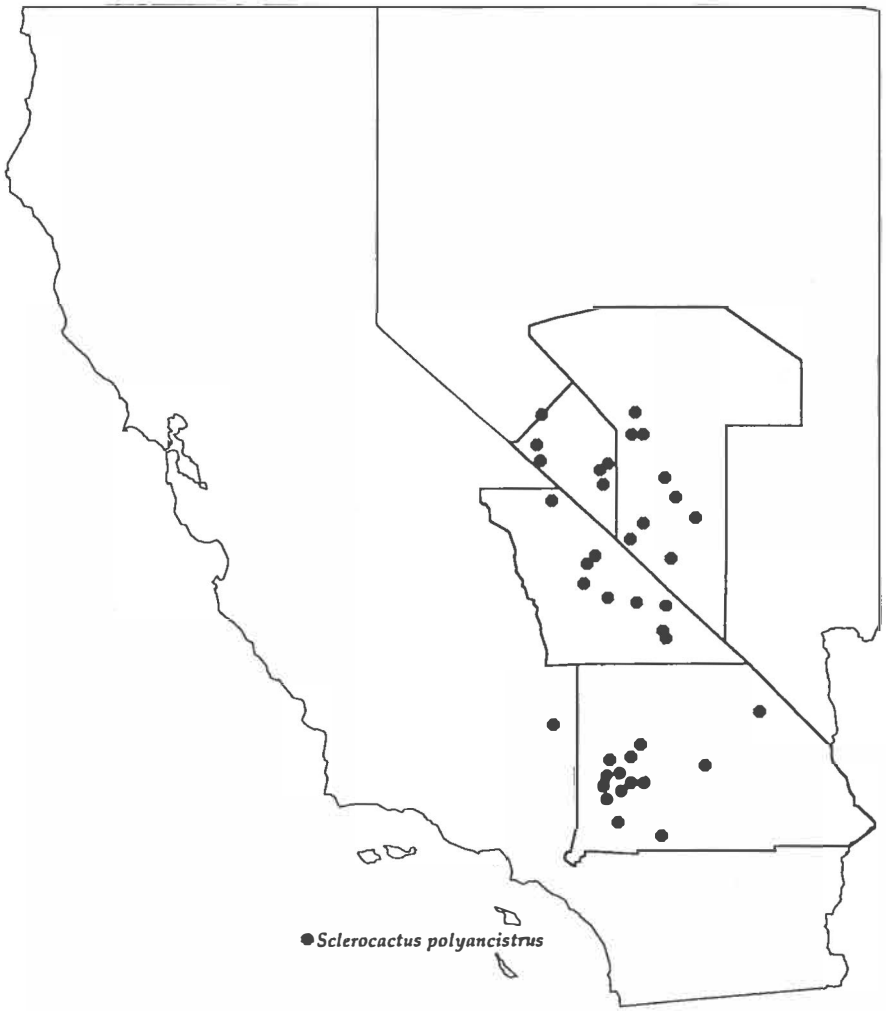

Fig. 26. Distribution of *S. polyancistrus* in California and Nevada based on herbarium collections. Maps by J. Mark Porter.

the type specimen coming from Cathedral Gorge State Park near Panoca, Nevada. *S. blainei* was described in 1985 by Welsh and Thorne, with the type specimen from near Currant, Nye County, Nevada. There are not enough differences between *S. schlesseri* and *S. blainei* to warrant taxonomic status for *S. schlesseri*, therefore it is reduced to synonymy.

Hochstätter (1993c) implies that *S. nyensis* was originally described by Welsh and Thorne in 1985 as *S. blainei*, which Hochstätter considers a hybrid between *S. polyancistrus* and *S. schlesseri*. The *S. nyensis* that Hochstätter describes is not the same material as that found at Currant (*S. blainei*). Therefore, *S. nyensis* represents a species different from *S. blainei*.

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References

Alberch, P., and J. Alberch. 1981. Heterochronic mechanisms of morphological diversification and evolutionary change in the neotropical salamander *Bolitoglossa occidentalis* (Amphibia: Plethodontidae). J. Morphol. 167:249–264.

———, S. Gould, G. Oster, and D. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296–315.

Arp, G. 1972. A revision of *Pediocactus*. Cact. Succ. J. (U.S.) 44:218–222.

Benson, L. 1950. The cacti of Arizona, 2nd ed. University of Arizona Press, Tucson, Arizona.

———. 1951. The Mesa Verde cactus. Leafl. West. Bot. 6:163.

———. 1966a. A revision of *Sclerocactus*. I. Cact. Succ. J. (U.S.) 38:50–57.

———. 1966b. A revision of *Sclerocactus*. II. Cact. Succ. J. (U.S.) 38:100–106.

———. 1974. New taxa and nomenclatural changes in the Cactaceae. Cact. Succ. J. (U.S.) 46:79–81.

———. 1982. The cacti of the United States and Canada. Stanford Univ. Press, Stanford, California. 1044 pp.

Berger, A. 1929. Kakteen. Eugen Ulmer, Stuttgart. 346 pp.

Boissevain, C. H., and C. Davidson. 1940. Colorado Cacti. Abbey Garden Press, Pasadena, California.

Britton, N. L., and J. N. Rose. 1922. *Sclerocactus*, in The Cactaceae, Vol. 3:212–215. Carnegie Inst. Wash. Publ. 248.

Busek, J. 1979. Die Gattung *Sclerocactus* Britt. & Rose. Kakt. and Sukk. 30:112–115.

———. 1983. *Sclerocactus pubispinus* and *Sclerocactus spinosior*. Kakt. and. Sukk. 34(2):34–38.

Castetter, E. F., P. Pierce, and K. H. Schwerin. 1976. A new cactus species and two new varieties from New Mexico. Cact. Succ. J. (U.S.) 48:138–139.

Clover, E. 1938. The Cactaceae of southern Utah. Bull. Torrey Bot. Club 65:397–412.

———. 1942. A new species and variety of *Sclerocactus* from Arizona. Amer. J. Bot. 29:172–174.

———, and L. Jotter. 1941. Cacti of the canyon of the Colorado River and tributaries. Bull. Torrey Bot. Club 68:409–419.

Coulter, J. M. 1896. Preliminary revision of the North American species of *Echinocactus, Cereus,* and *Opuntia*. Contr. U.S. Nat. Herb. 3:355–462.

Earle, W. H. 1980. Cacti of the Southwest. Desert Botanical Garden, Phoenix, Arizona.

Engelmann, G. 1856 (1857, but preprint issued in 1856). Synopsis of the Cactaceae of the territory of the United States and adjacent regions. Proc. Amer. Acad. 3:259–346.

———. 1863. Additions to the cactus-flora of the territory of the United States. Trans. Acad. Sci. St. Louis 2:197–204.

Evans, J. Whitman. 1939. A new species. Cact. Succ. J. (U.S.) 11:74–76.

Gould, S. J. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, Massachusetts.

Guerrant, E. O. 1982. Neotenic evolution of *Delphinium nudicaule* (Ranunculaceae): a hummingbird-pollinated larkspur. Evolution 36:699–712.

Heil. K. D. 1979. Three new species of Cactaceae from southeastern Utah. Cact. Succ. J. (U.S.) 51: 25–30.

———, B. Armstrong, and D. Schleser. 1981. A review of the genus *Pediocactus*. Cact. Succ. J. (U.S.) 53:17–39.

———, and J. M. Porter. 1987. A taxonomic evaluation of *Sclerocactus glaucus* and its relationship to *Sclerocactus parviflorus*. Unpublished report on file with the U.S. Fish and Wildlife Service, Salt Lake City, Utah. 32 pp.

———, and S. L. Welsh. 1986. New *Sclerocactus* (Cactaceae) from Nevada. Great Basin Naturalist 46:677–678.

Hennig, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.

Hochstätter, F. 1989. Nieubeschrijving *Sclerocactus wetlandicus* species nova- Een nieuwe *Sclerocactus* uit Uintah County, Utah, USA. Succulenta 68: 123–126.

———. 1992. Revision *Sclerocactus* I. Succulenta 71: 247–262.

———. 1993a. Revision *Sclerocactus* II. Succulenta 72:19–34.

———. 1993b. Revision *Sclerocactus* III. Succulenta 72:82–92.

———. 1993c. Revision *Sclerocactus* IV. Succulenta 72:137–140.

———. 1993d. Revision *Sclerocactus* IV. Succulenta 72:187–191.

———. 1993e. The genus *Sclerocactus* revised (magnificent, fascinating natural wonder). Mannheim, Germany.

Hunt, D., and N. Taylor. 1986. The genera of the Cactaceae: towards a new consensus. Bradleya 4:65–78.

Lord, E. M., and J. P. Hill. 1987. Evidence for heterochrony in the evolution of plant form. *In* R. A. and E. C. Raff, eds., Development as an evolutionary process. Alan R. Liss, Inc., New York.

Marshall, W. T., and T. M. Bock. 1941. Cactaceae. Abbey Garden Press, Pasadena, California. 227 pp.

Mason, H. L. 1946a. The edaphic factor in narrow endemism. I. The nature of environmental influences. Madroño 8:209–240.

———. 1946b. The edaphic factor in narrow endemism. II. The geographic occurrence of plants on highly restricted patterns of distribution. Madroño 8:241–257.

Peebles, R. H. 1949. Studies in Arizona Cactaceae. Leafl. West. Bot. 5:191–192.

Pinkava, D., L. McGill, T. Reeves, and M. McLeod. 1977. Chromosome numbers in some cacti of western North America. II. Bull. Torrey Bot. Club 104:105–110.

Purpus, J. A. 1895. *Echinocactus glaucus*. Monatsschr. Kakteenk. 5:106.

———. 1925. *Echinocereus whipplei* Engelm. & Bigelow var. *glaucus*. Mitt. Deutsch. Dendr. Gesellsch.

Schelle, E. 1907. Handbuch der Kakteenkultur. Stuttgart.

Welsh, S. 1984. Utah flora: Cactaceae. Great Basin Nat. 44:52–69.

Welsh, S. L., N. D. Atwood, L. C. Higgins, and S. Goodrich. 1987. A Utah flora. Great Basin Naturalist Memoir No. 9. Brigham Young University.

———, ———, ———, and ———. 1994. A Utah flora. Great Basin Naturalist. Brigham Young University.

———, and K. Thorne. 1985. A new *Sclerocactus* from Nevada. Great Basin Naturalist, 45:553–555.

Woodruff, D., and L. Benson. 1976. Changes of status in *Sclerocactus*. Cact. Succ. J. (U.S.) 48:131–134.

Woodson, D. 1974. 2 *Sclerocactus* species in the west desert of Utah and adjacent Nevada. Int. Congr. Evol. Biol. 1. Boulder, Colorado. 228 pp.